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A Comparative Study Of The Use Of Habitat By Arctic Loons And Red-throated Loons

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A COMPARATIVE STUDY OF THE USE OF HABITAT BY ARCTIC LOONS AND RED-THROATED LOONS

by

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ABSTRACT

The use of space by Arctic Loons (Gavia arctica) and Red-throated Loons (Gavia stellata) was compared on structurally simple tundra study areas at the McConnell River, Northwest Territories.

Differential habitat selection by the two species was based on nest pond size. Other features of ponds were unimportant. Each species preferred 'island-type' nests but this did not limit the population. Arctic Loons chose the largest ponds whereas Red-throated Loons used small ones. Red-throated Loons did not use larger nest ponds at Harrington Harbour, Quebec where Arctic Loons did not occur which suggested that Red-throated Loons were not restricted to small ponds at the McConnell River by competition with Arctic Loons. The structure and behaviour of Red-throated Loons adapted them to small ponds. These ponds thaw first and are the only ones suitable for loons in the short frost-free summers of the high arctic. Red-throated Loons occur farther north than all other loon species. It is suggested that a common ancestor of Arctic and Red-throated Loons was isolated into two populations by the Pleistocene ice sheets. The ancestor evolved into the Red-throated Loon in a cold arctic refugium and the Arctic Loon south of the ice.

Each loon species defended territories which appeared constant from year to year. Arctic Loons selected territories of a certain size whereas Red-throated Loons selected for the number of individual ponds per territory. These differences were correlated with the fact that Arctic Loons gathered food for their young on the territory while Red-throated Loons did not but used the extra ponds for escape from predators. Large Arctic Loon territories were used most often and were most successful. The few Red-throated Loon territories with only one pond were rarely successful. Territorial defense was not a major drain on the time budget of loons. Territories were apparently selected in summer prior to first nesting. All Arctic Loon habitat was occupied. Only coastal Red-throated Loon habitat was fully occupied but territory size was the same in all parts of the study area. Territorial behaviour by Red-throated Loons forced some pairs to nest in areas away from the coast where they were less successful than pairs near the coast.

Arctic Loons dominated Red-throated Loons during the rare interspecific interactions. Red-throated Loons nesting on larger than average ponds were more likely to have interactions with Arctic Loons and interspecific competition may reinforce the habitat selection for small ponds by Red-throated Loons.

The suitability of various areas of equal structural

habitat depended on their distance from coastal food sources. When food was equally available it seemed that fox predation controlled Red-throated Loon distribution. The ecological basis of chick growth affected the distance from food sources at which Red-throated Loons could nest.

Each loon species usually laid two eggs which hatched asynchronously. The first hatched Red-throated Loon survived better and grew faster than its sib. These differences were facilitated by a dominance hierarchy which insured that the first hatched chick received sufficent food before its sib got any. First hatched members of broods of two survived and grew as well as broods of one indicating that the second young had no detrimental effects on the first hatched. Similar patterns seemed to occur in Arctic Loons. Red-throated Loons apparently utilized a fluctuating food source and asynchronous hatching was an adaptation to it as indicated by different growth rates, feeding rates and early chick survival in two years.

Both species had the same clutch size and hatching success but Arctic Loons were more successful at raising young. This was correlated with food sources.

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INTRODUCTION

The factors which influence the number of species in a community and the number of individuals in each species, are of prime importance in population ecology. These factors can be profitably examined by comparing closely related species in simple natural ecosystems.

The tundra ecosystems of arctic regions are relatively simple in terms of their unidimensional structure, the small number of species, and the shortness of their food chains. These high latitude areas have a harsh climate which stops virtually all primary production for 8 to 9 months of the year. This harshness places severe constraints upon the flexibility and variety of possible adaptations available to a species inhabiting this environment.

The Arctic Loon (Gavia arctica) and the Red-throated Loon (Gavia stellata) are closely related congeneric bird species of nearly equal size. They are marine species except during the breeding season when they nest on freshwater ponds. Both must utilize such ponds and are potential competitors for this resource. This is a study of how the two species partitioned this habitat.

The first step was to document what habitat was selected by each species and what aspects of this habitat were critical for each species. It was then possible to

determine how each species was distributed throughout its preferred habitat and the role of territorial behaviour in effecting this distribution.

Interspecific behaviour between the two loons was analyzed and then its effects were compared with the role of habitat selection in an attempt to determine the relative importance of each factor with respect to the habitat separation by the two species.

It was necessary to consider the factors which control the number of individuals in each species as population density surely influences the use of space by an animal species. The reproductive biology of both loons was documented and factors affecting the reproductive potential of each species (i.e. clutch size and brood success) were assessed. Lack of available food and adaptations to counteract such a shortage were potentially important factors affecting the distribution of Arctic and Red-throated Loons, and these adaptations were examined.

It was hoped that a comparative study of the above factors would provide an understanding of why and how the Arctic and Red-throated Loons shared the tundra habitat.

METHODS

The study was carried out on the coastal plain of Hudson Bay at the mouth of the McConnell River (60°50'N, 94°25'W), Keewatin District, Northwest Territories (figure 1). A 16.5 km^2 study area was used. It had been surveyed for studies of Canada Geese (Branta canadensis) by Dr. C.D. MacInnes and his students. This main study area was subdivided into 3 plots (A, B, and C) of 4 km^2 each and a fourth plot (D) which was 4.5 km^2 (figure 2). Three summers (mid-May to mid-August of 1967-68-69) were spent there.

The main study area was flat, wet tundra with numerous ponds and wet marshy areas (figure 3). Most of the dry portions of these marshes were less than 2 ft above summer water level (MacInnes 1962) and the whole area was underlain by permafrost which prevented downward drainage through the soil.

Data on loons and their habitat were gathered in several ways. Loons were observed from two elevated observation blinds (figure 4). The upper portions of these towers were 8 X 8 X 8 ft and they enabled the observer to live in them and to make unobstructed observations for extended periods without disturbing the birds. The tower in area C was within telescope viewing distance of 9 Arctic Loon and

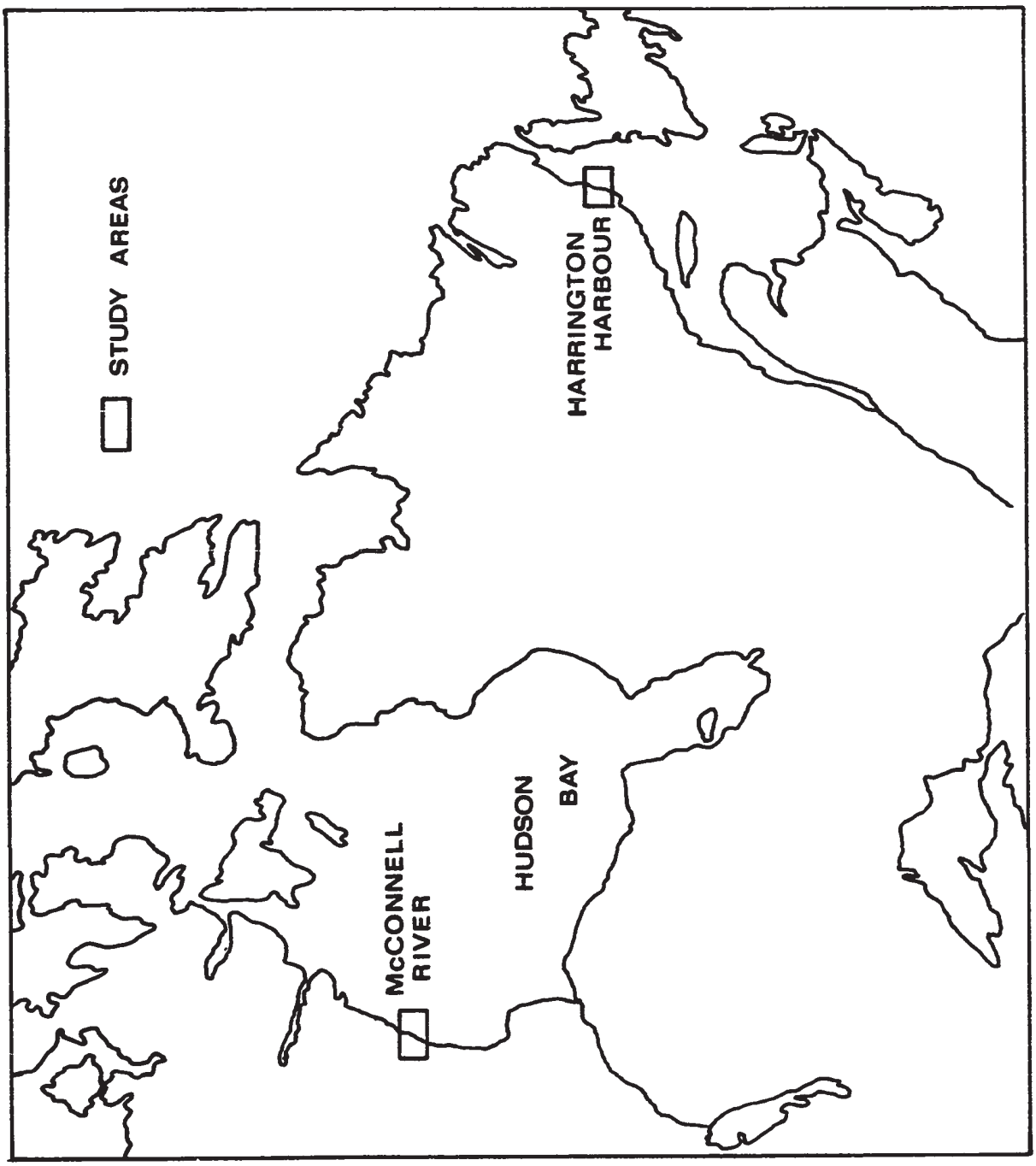

Figure 1. Location of study areas. The McConnell River was studied in 1967, 1968, and 1969 and Harrington Harbour was surveyed in 1970.

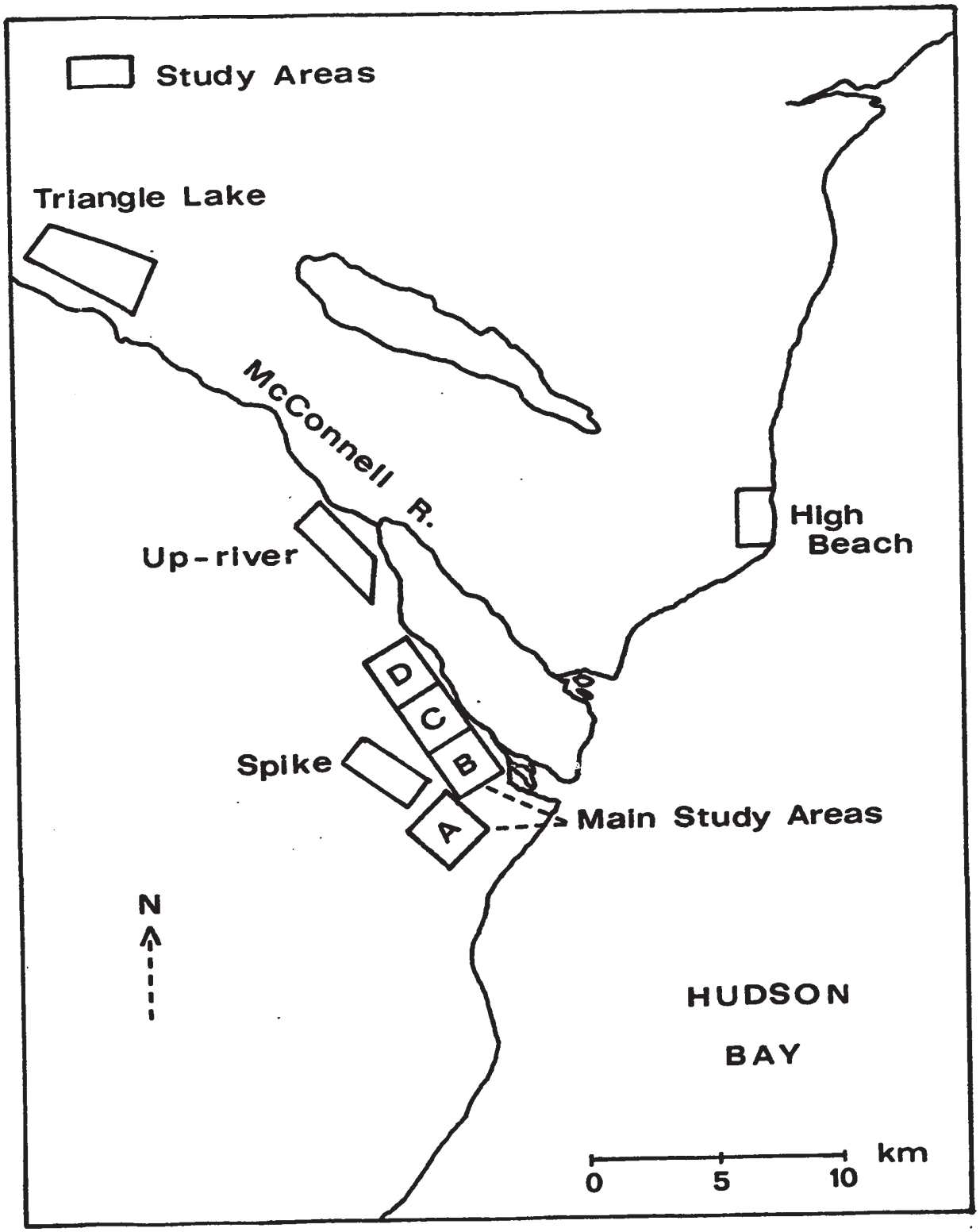

Figure 2. Location of study areas at the McConnell River, N.W.T.

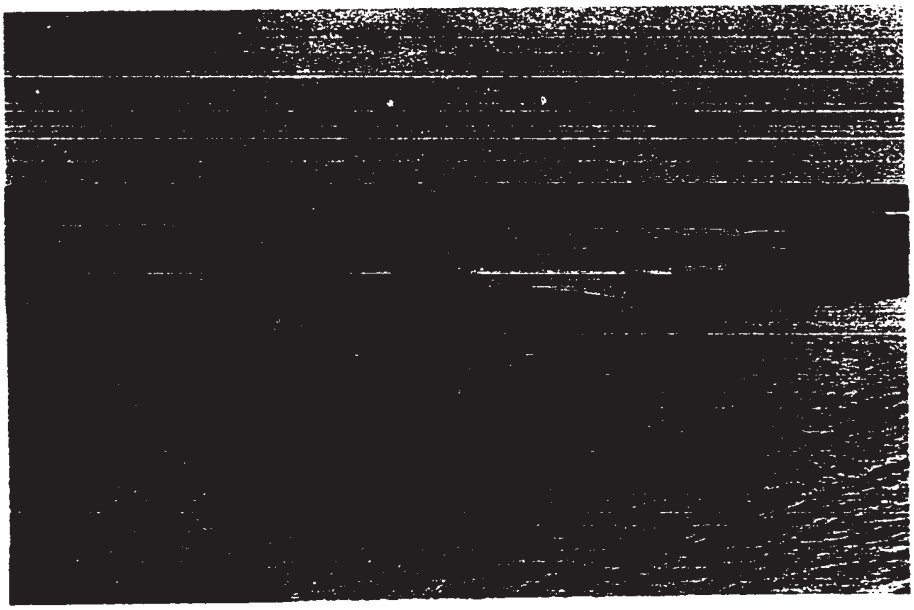

Figure 3. Typical flat loon habitat at the McConnell River, N.W.T.

Figure 4. Tower blind used for observing loons at the McConnell River, N.W.T.

Figure 3. Typical flat loon habitat at the McConnell River, N.W.T.

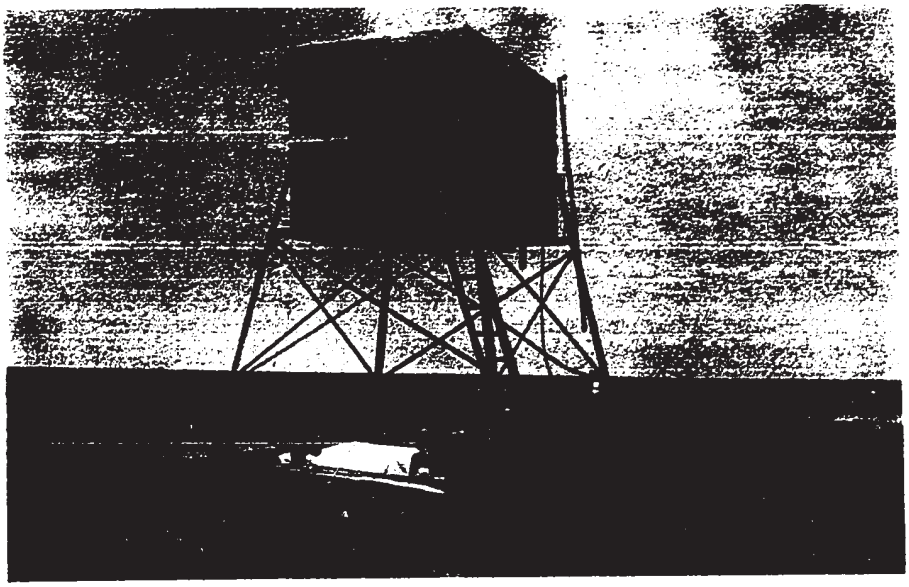

Figure 4. Tower blind used for observing loons at the McConnell River, N.W.T.

7 Red-throated Loon territories while the tower in area D was within range of 7 Arctic Loon nests. The observation towers were generally ignored by birds in the area and a Willow Ptarmigan (L. lagopus) nested 3 ft from the base of the tower in area C.

Every pond on the main study area was visited and searched for nests at approximately 10 day intervals until hatching of the eggs when visits were made more frequently. Every sighting of loons and their nests was recorded on maps drawn from aerial photographs.

The area, length and width of all ponds were determined from aerial photographs. Pond length was the maximum straight unobstructed expanse of water. Pond width was the maximum unobstructed distance at an angle of between 65° and 115° with the line measured for pond length. A loon must run across the water in order to take off. Thus, length and width were potentially important in allowing it to take flight into a wind from any quarter. Ponds were also examined for various features such as type of shoreline, bottom type, and visibility.

Four other study areas were surveyed in the McConnell River area (figure 2). They were compared with the main study area and this allowed an assessment of the relationship of breeding distribution to distance from the Hudson Bay coast. These 4 areas were selected from aerial photographs to be representative of the surrounding habitat and contained

ponds apparently suitable for both Arctic and Red-throated Loons.

The Triangle Lake study area was a typical area of lakes, about 25 km inland from the main study area. The average pond size was 18.39 ha. This area was surveyed on 1 July 1969 when the larger lakes were still up to 30 or 40 per cent ice covered. No measurements were taken but the larger lakes were probably much deeper than in the main study area.

The Spike study area was located on a drier, upland tundra region and contained several large lakes as well as small ponds. The primary survey was done in 1967 but casual observations in 1968 and 1969 indicated similar use patterns in all years. These lakes were not as deep as those in the Triangle Lake area but were deeper than those on the main study area.

The 'Up-river' survey area was very similar to the main study area with a large number of suitable ponds. The depth of the ponds was the same in each area and the general bottom and shoreline configuration were similar in the two areas. The Up-river survey area was close to the McConnell River and would be flooded every spring, as in the main study area. The area was surveyed on 4 July 1969.

The fourth survey area was located at the Hudson Bay coast behind a high beach ridge. The 'High Beach' area was on contiguous water area of approximately 165 ha. It had a

uniform sandy bottom and a depth of less than one metre. The water surface was subdivided by over a hundred small islands (from 1 X 1 m to over 1 ha in size). The area was thus effectively divided into nearly 40 sub-ponds. The High Beach area was surveyed on 26 June and 2 July 1969.

Three weeks in July 1970 were spent near Harrington Harbour, Quebec, on the North Shore of the Gulf of St. Lawrence (figure 1). Eleven study areas (figure 5) were censused to provide data on breeding distribution of Red-throated Loons in an area where Arctic Loons did not occur.

Details of specific methods will be presented where appropriate.

Statistical tests are standard ones from Steel and Torrie (1960), Snedecor and Cochran (1967), and Sokal and Rohlf (1969). The 0.05 probability level was the minimum level of significance. Tests which yielded not significant results are noted by NS.

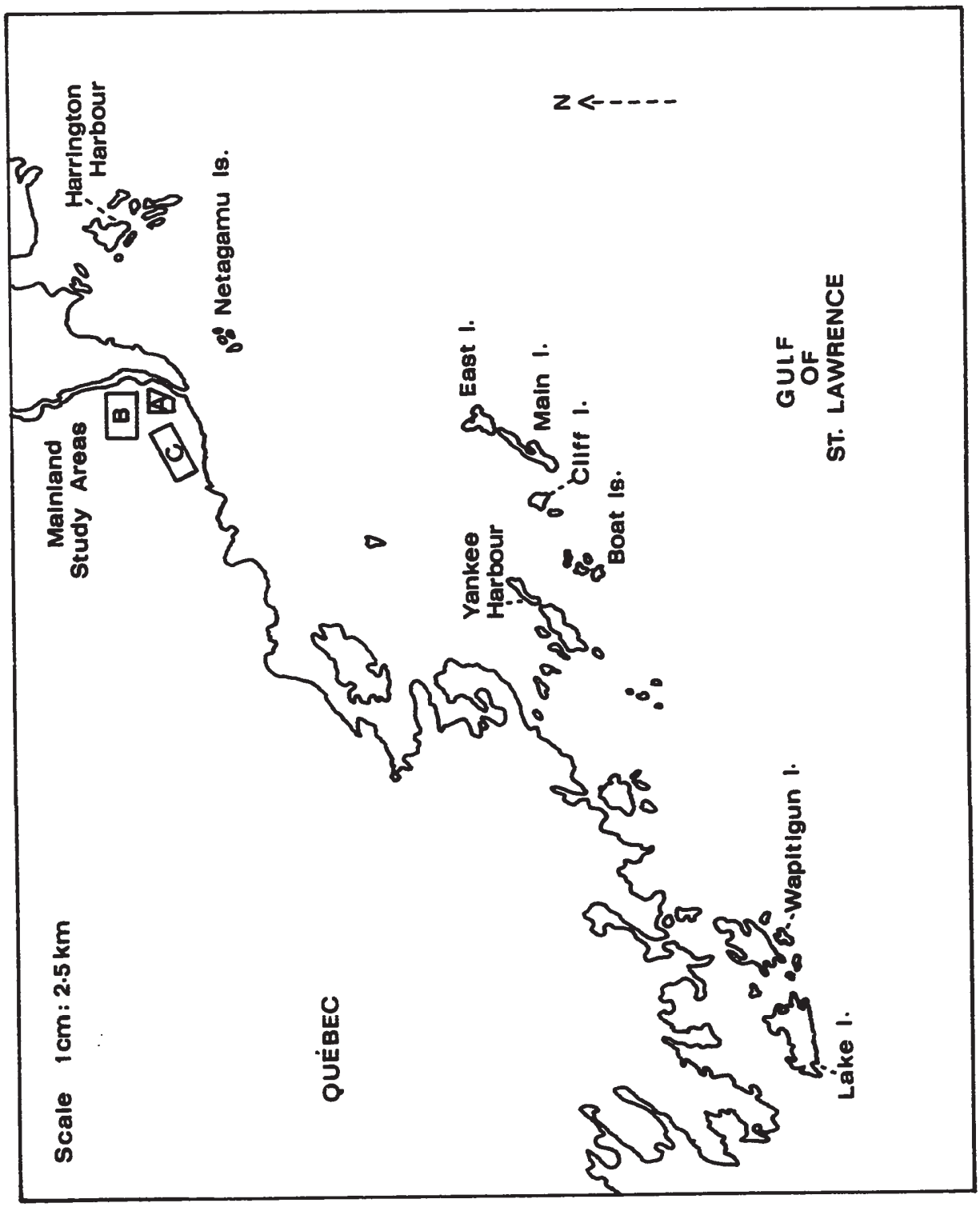

Figure 5. Location of study areas at Harrington Harbour, Quebec. The three mainland areas and eight named islands and island groups were studied.

I. HABITAT SELECTION BY LOONS

Arctic and Red-throated Loons are generally similar in size and habits so that detailed analyses of the nesting requirements of each species were necessary to elucidate the critical factors needed by each species.

The basic method of determining which features of ponds were selected by a loon species involved comparing the ponds that it used with those that it did not use. Used ponds should have different characteristics than non-used ponds. If there were no differences in the two groups then it was likely that no selection for pond characteristics was occurring.

I.1. ARCTIC LOON NEST PONDS

I.1.A. Pond Size

The effect of pond-size can only be isolated after the importance of several other parameters has been taken into account. These potential factors are discussed in later sections. The tundra ponds at the McConnell River study area were very uniform, except for size, and this minimized the importance of these subsidiary characteristics. In the rare cases when such factors were important they were considered.

In the main study area (16.5 km^2) at the McConnell

River there were 250 pond areas ranging in size from 0.07 to 21.37 ha. There were really about 220 distinct ponds but some of the larger ponds were divided by islands and points so that there were in effect several pond areas and potential loon territories within some large ponds. The largest pond (21.37 ha) had 5 Arctic Loon nests in 1967.

In any one year about 35 pairs of Arctic Loons resided in this area and they presumably selected the most suitable ponds.

Table 1 compares the size of ponds used for nests in the three years of the study. The variability of the used ponds was the same for the respective measurements in each year. The mean pond size was the same in each year, ranging from 2.13 to 2.73 ha. The average pond length and the average pond width were respectively the same in each year. The Arctic Loons selected the same size characteristics for nest ponds in each year.

The 94 nests in table 1 represent 46 different nest ponds. These ponds are partitioned in table 2 into those used in all three years and those ponds used in only one year. The thrice-used ponds included 7 which had nests in two years and the pair used them as part of their territories in the third year. The multi-used ponds were strikingly larger than the single-used nest ponds. These differences hold for area, length and width (table 2). On the assumption that birds use the best habitat most often, then it is safe

TABLE 1

SIZE OF PONDS WITH ARCTIC LOON NESTS - McCONNELL RIVER, N.W.T.

		1967	1968	1969	F-max[1]	F-anova[2]
No. of nest ponds		34	27	33		
Area (ha)	Mean	2.73	2.13	2.58	1.846^{ns}	$<1^{ns}$
	S.D.	2.269	1.723	2.341		
Length (m)	Mean	252.50	231.33	242.61	1.710^{ns}	$<1^{ns}$
	S.D.	111.811	85.499	105.336		
Width (m)	Mean	148.56	129.33	136.64	2.143^{ns}	$<1^{ns}$
	S.D.	64.269	46.410	67.942		

1. F-max test of equality of sample variances.

2. ANOVA for equality of means.

TABLE 2

COMPARISON OF ARCTIC LOON NEST PONDS USED IN THREE YEARS VERSUS PONDS USED IN ONLY ONE YEAR

		Multi-used Ponds	Single-used Ponds	Variance[1] (F)	Mean[2] (t)
No. of Nest Ponds	N	30	13		
Area (ha)	Mean	2.88	0.83	15.9**	4.427*
	S.D.	2.371	0.594		
Length (m)	Mean	271.30	158.69	3.596*	3.679**
	S.D.	130.841	68.994		
Width (m)	Mean	150.20	100.77	2.185[ns]	2.521[*3]
	S.D.	64.400	43.572		

* P<0.05; ** P<0.01

1. Variance ratio to test equality of 2 sample variances (F is two-tailed).
2. T-test for equality of means with samples of unequal variance.
3. T-test for samples with equal variance.

to conclude that the Arctic Loons were selecting the larger ponds.

The small once-used ponds were often part of a larger loon territory consisting of 2 or 3 ponds. Arctic Loons defend these extra ponds and use them for preening, loafing, escape and occasionally they may move their young onto them. These ponds are integral components of the territory and are unavailable to other loons.

I have assumed that multi-used ponds were used by the same pair in each year. This is suggested by the constancy of territory boundaries and use throughout the study. Loons are long-lived (Palmer 1962; Salmonson 1961, 1965; Nordstrom 1960) and have a very low recruitment rate judged by the low production of young in this study which indicated that there was very little turnover in the population. There also seemed to be similarities in the behaviour of the birds on certain territories from year to year. Thus, the assumption that the same pairs regularly occupied the same territories was probably justified although the following analyses in no way depend on it. Other workers have made the same finding (Lehtonen 1965, 1970; Dement'ev et al. 1968).

Arctic Loons used 46 ponds for nests in the main study area. Only 28 of the 200 suitable ponds (4 ponds had unsuitable shoreline - section I.1.B) not used for nests by Arctic Loons were over 0.75 ha in area. Nineteen of these 28 were part of Arctic Loon territories. The largest of the

remaining 9 ponds was only 1.46 ha. Arctic Loons were selecting the largest available ponds and they were using them all.

It remains to be shown whether Arctic Loons could have used the vacant smaller ponds. What are the minimum size requirements for a nest pond? This becomes confused with what constitutes a minimum territory size (section II). A small pond may be used for nesting if the pair has access to nearby larger ponds.

The smallest nest pond was 0.225 ha in area, 100 m long and had a maximum width of 50 m. This is probably close to the minimum size of pond which Arctic Loons can use. In calm circumstances an Arctic Loon requires 30 to 50 m of open water in which to take off. It could not safely use a smaller pond. The pair using the smallest pond also used a larger nearby pond (0.81 ha) for escape when disturbed. This nearby pond had been used for nests in the two previous years and likely would have been used in 1969 as well, except that it remained ice covered until late June and the pair used the smaller pond which thawed earlier. This use of small ponds, when the larger regularly used nest ponds were late thawing, occurred in 3 cases in the delayed spring of 1969. The other 2 small nest ponds were 0.495 ha in area.

Arctic Loons were capable of nesting on small ponds but actually selected the largest pond areas available. They used small ponds only in conjunction with nearby large ones.

I.1.B. Shoreline and Nest Site

The shoreline of a pond can influence the suitability of that pond for loons. This section considers whether shorelines were physically suitable for nest sites and if so how this affected pond selection by Arctic Loons.

Shoreline operated on two levels, an absolute level, where the shore was such that nesting was impossible and a relative level, where variation in shoreline led to degrees of suitability. The first level involved shorelines which were too steep and high. Since loons are almost immobile on land, and normally cannot take flight from it, they nest on low, flat areas adjacent to water. If a shoreline was too steep, then a loon could not climb up it or nest on it. There were only four ponds in the main study area which had unsuitable shorelines (i.e. 1.6% of all ponds). Two small ponds had very steep banks with no possible location for a nest. Two other large ponds (1.26 and 2.47 ha) were unsuitable because of rocky shores consisting almost entirely of small boulders. These four ponds are not considered in any of the analyses in this study.

Was there a hierarchy of suitability when some shoreline was suitable for nesting? Were certain types of shore preferred for nesting?

i) Nest substrate

Shorelines suitable for nests were classified into four broad categories: islands, points, dry shore, and wet

grassy areas. An island was any area of land surrounded by open water. The island had to have at least one ledge suitable (flat, large enough for a sitting adult, and at water's edge) for a nest. Points were mainland areas which protruded into a pond, were clearly surrounded by water on three sides and had low, flat areas suitable for nests. Dry shoreline was any area with a clear demarcation between dry land and water's edge and having a potential nest site. Wet grassy areas were regions of shallow water (10 to 30 cm in depth) with a growth of emergent grasses and sedges leading to an indistinct boundary between dry shore and open water. Loons which nested in such areas built up a nest platform of mud and aquatic vegetation in the shallow water. These nests were usually closer to open water than to dry land. They were, in effect, loon-made islands.

Nests on dry substrate were mere scrapes on flat ground. The loon placed a little wet vegetation around the rim of the scrape and its body weight compressed the central part of the nest forming a very shallow saucer-like surface for the eggs.

The presence or absence of the four shoreline types was noted for each nest pond. A pond was recorded as having dry shore or wet grassy shoreline types only if several metres of unbroken habitat were present. The mere presence of an island or point was sufficient to be recorded, regardless of its percentage of total shoreline.

Table 3 compares the number of nest ponds containing

TABLE 3

SELECTION OF NEST SUBSTRATE BY ARCTIC LOONS[1]

Substrate type and number of nest ponds with this substrate	Number of ponds with nests on							
	Dry Shore		Island		Point		Wet Grassy	
	N	(%)	N	(%)	N	(%)	N	(%)
Dry Shore - 97	8	(8.2)	70	(72.2)	8	(8.2)	11	(11.3)
Island - 85	1	(1.2)	70	(82.4)	8	(9.4)	6	(7.1)
Point - 52	2	(3.8)	38	(73.1)	8	(15.4)	4	(7.7)
Wet Grassy - 14	0	(0.0)	3	(21.4)	0	(0.0)	11	(78.6)

1. Based on 97 nesting attempts.

each substrate with the number and percentage of nests on each substrate type. For example, there were 97 nest ponds with dry shore and 70 (72.2%) of these had nests on islands but only 8 (8.2%) had nests built on dry shore. A pond used for 3 years is considered to be 3 separate ponds in this analysis since there was very little re-use of nest sites (table 5) and each nest attempt probably represented an independent choice of site. Table 3 indicates that islands were highly selected as nest sites (82.4% of ponds with islands had nests on islands). Wet grassy areas were also heavily used with 78.6% of the ponds with wet grassy areas having nests on these areas. Of the 9 nest ponds with both islands and wet grassy areas, 6 had nests in wet grassy areas and 3 had nests on islands. Considering nests in wet grassy areas as loon-made islands, 81 of 97 nests (83.5%) were on islands.

The remaining 16 nests included 8 on points and 8 on dry shoreline. The points resemble islands in that they were surrounded by water on three sides. There were 52 nest ponds with both points and dry shoreline and 8 of these had nests on points and only 2 on dry shore. Of the 8 nests on dry shore, 5 were on ponds in which only dry shore was available and another 2 were on ponds with only points and dry shore. The other pond also had islands. Therefore in 7 of 8 ponds with nests on dry shore there were no islands or wet grassy areas available.

There was strong selection for islands and wet grassy

areas for nests. However, the presence of 16 nests on mainland (shore and points) suggests that islands are not essential components of Arctic Loon nest ponds.

In spite of this selection for islands and wet grassy areas, breeding success on mainland nests was higher than that of island and wet grassy area nests (0.81 young/nest versus 0.58 young/nest respectively) although this difference was not significant ($\chi^2 = 1.92$, df = 2, for the H_o of equal numbers of nests producing 0, 1, and 2 young, for each group; i.e. H_o: 5:9:2 = 38:35:5).

The Common Loon (Gavia immer) also has been shown to prefer island nest sites (Olsen and Marshall 1952; Mathison 1969).

ii) Nest island characteristics

Islands were highly selected for nest use by Arctic Loons. I measured 38 nest islands which were used a total of 54 times over the 3 year period. The data are presented in table 4 and are grouped according to the number of years the islands were used for nests.

The nest islands ranged in size from 2 ft by 2 ft (61 cm X 61 cm) to 350 ft X 150 ft (106.7m X 45.7m). On the assumption that islands used more than once were preferred over once-used islands, these groups were compared for size differences. Data from table 4 were grouped into islands used only once (25) and those used more than once (13). Mean

TABLE 4

SIZE OF ARCTIC LOON NEST ISLANDS

No. of Years islands used for nests	No. of Islands	Length (ft)		Width (ft)	
		Mean	S.D.	Mean	S.D.
3	3	44.3	36.005	24.0	18.520
2	10	54.4	58.306	19.5	22.071
1	25	39.7	72.691	20.5	35.196

lengths of the two groups were not significantly different ($t = -0.454$; $df = 36$; P is NS) and mean widths were not different ($t = 0.0016$; $df = 36$, P is NS). There was no difference between the two groups and it appeared that the size of the island was not important to Arctic Loons.

It is interesting that fully 25 of 38 islands were used in only one year indicating that selection was for islands in general rather than for specific islands. Any island was suitable if it had a low, flat ledge near the water. The size and shoreline of the rest of the island were apparently immaterial to the loons.

iii) Nest site fidelity

Arctic Loon territories were very stable from year to year (section II). The same ponds and groups of ponds were occupied, presumably by the same pairs. If nest sites and shore suitability were limiting factors in nest selection then it is probable that pairs would be faithful to these limited sites.

It is obvious from table 5 that there was little fidelity to nest sites from year to year. In the 33 areas represented there was a potential maximum of 91 nest sites if no site was re-used and a potential minimum of 33 sites if all sites were re-used. In fact, 84 different sites were used. It seems safe to say that available nest sites were in no way limiting this population of Arctic Loons.

TABLE 5

FIDELITY TO NEST SITE BY ARCTIC LOONS

	No. of pond areas	No. of pond areas with same nest site in 3 years	No. of pond areas with same nest site in 2 years	No. of pond areas with different site in all years
Pond areas used in 3 years	25	1	5	19
Pond areas used in 2 years	8	-	0	8

I.1.C. Other Factors

There are several other features of ponds which are of potential importance to Arctic Loons and these are discussed in the following sections.

i) Pond depth

The depth of a pond may have two effects on its suitability for Arctic Loons. First is the effect of depth on the food organisms utilized by the loons (section I.1.C.iii). Second is the effect of depth on the escape behaviour of the loons, particularly the chicks. Escape behaviour of loon chicks is discussed in section I.2.C.i.

Pond depth was of limited importance at the McConnell River since all ponds were of a similar depth with virtually flat bottoms. The average depth of 19 Arctic Loon ponds was 52 cm with a range of 30 to 90 cm (based on 5 approximately equally spaced depth measurements taken while wading across the pond). At the McConnell River it appeared that about 30 cm was the minimum acceptable modal depth for an Arctic Loon nest pond. Virtually all ponds in the study area exceeded this depth. The maximum depth of any pond on the study area was about 1 m. Arctic Loons used deeper ponds and lakes in Scandinavia (Lindberg 1968; Lehtonen 1970).

ii) Bottom type

The colour and texture of the pond bottoms may have an effect on pond suitability. This could work through

selection for escape behaviour of chicks when threatened by a predator and will be discussed in section I.2.C.i.

iii) Food supply

At the McConnell River all adult Arctic Loons fed on Hudson Bay. However, on the main study area, the adults fed the young primarily with food gathered in the nesting territories. This included Nine-spined Stickleback (Pungitius pungitius), small Grayling (Thymallus thymallus), fairy shrimp (Order Anostraca sp.), tadpole shrimp (Order Notostraca sp.), and other, unidentified invertebrates.

Food in the nest pond was very important to the survival of young Arctic Loons (section V), which raises the question of whether ponds with food were selected or was the presence of food a fortunate coincidence?

There was no food available in the ponds when the Arctic Loons set up territories in the spring,since the whole area was flooded and the pond bottoms were still ice-covered. However, it is likely that loons selected their territories in the previous summer (Appendix 1) and in this way the birds could learn about the normal presence of food in the pond.

Seven pairs of Arctic Loons nested on the High Beach study area (fig. 2) in 1969 and fed their young on fish caught in Hudson Bay. The same was true for two pairs which I watched at Eskimo Point in August 1968 and 1969. These areas were

very close to Hudson Bay. The High Beach area had a uniform sandy bottom and very little food. No fish or invertebrates were seen during two full days of wading in the area. This indicates that food on the nest territory was not an essential requirement for nesting if an alternative food-source was available nearby (see also Snyder 1957).

It was not possible to compare the fledging success of young Arctic Loons fed from Hudson Bay and those fed on food gathered on the nesting territory. A relevant comparison is the success of Arctic Loons on the main study area with Red-throated Loons from the same area. The Arctic Loons used food from the nest territories and the Red-throated Loons used food from Hudson Bay. The data are analyzed in section V where the lower fledging success of Red-throated Loons is correlated with lower food availability. It seems probable that Arctic Loons which relied on food from Hudson Bay would also have had reduced success.

iv) Visibility from the nest pond

There are two strategies available to a nesting loon with regard to the placement of nests. A loon can nest in the open and command an unobstructed view of its surroundings, or it can hide its nest.

The terrain at the McConnell River was flat and all potential nest sites commanded unobstructed views of the surrounding area. It was not possible for a loon to hide its nest in this region.

v) Protection of nest from wave action

Artic Loons nest at water's edge and it is possible that wave action could threaten the nest and eggs. All ponds on the main study area were small enough that wave action did not threaten loon nests.

Some of the nest lakes on the 'spike' survey area (figure 2) were very large. Two nests were found on a lake 365 ha in area and 2.6 km by 2.1 km. Both nests were in small protected bays and none were found on the main, exposed shore of the lake. This pattern was found on three other large lakes in the 'spike' survey area. On large lakes, nests of Arctic Loons were always on the lee side of points or islands and were not exposed to a large sweep of open water.

vi) Water clarity

Pejler (1962) and Lindberg (1968) considered that transparency of the water in nest ponds was important to nesting Arctic Loons in Sweden. There was little apparent difference in water clarity throughout the pond system at the McConnell River and Arctic Loons were thus unable to choose between ponds on the basis of clarity.

1.2. RED-THROATED LOON NEST PONDS

Red-throated Loons nested throughout the study area and nest pond-use was examined with the same techniques used to study Arctic Loon nest ponds.

I.2.A.i) Pond Size at the McConnell River

There were no differences in the areas, lengths or widths of nest ponds used by Red-throated Loons in each of the three years (table 6). This applies to both means and variances.

If certain pond sizes are favoured for nesting and these ponds are in short supply, then they will probably be used more often than the less suitable pond sizes. Nest ponds used in three, two, and only one year were compared with respect to size (table 7).

These data show that multi-used nest ponds were no different than single-used ponds in terms of the means and variances of the three measurements. Furthermore, only 5 ponds were used in all three years and only 13 were used in two different years. This suggests that there was no shortage of ponds of suitable size for Red-throated Loons and all 67 nest ponds were equally suitable. This raises the question of how these ponds compared with those that were not used for nests.

There were 250 ponds on the main study area. Five of these ponds were unsuitable for loons of either species (2 were too rocky, 2 had banks which were too steep, and 1 always dried up in July). Sixty-five of the remaining 245 ponds were part of active Arctic Loon territories and were unavailable to Red-throated Loons due to behavioural interactions between the species. This leaves 180 ponds of which 67 were used for

TABLE 6

SIZE OF PONDS WITH RED-THROATED LOON NESTS - McCONNELL RIVER, N.W.T.

		1967	1968	1969	F-max[1]	F-anova[2]
No. of nest ponds		29	27	34		
Area (ha)	Mean	0.367	0.342	0.263	2.241^{ns}	2.012^{ns}
	S.D.	0.2750	0.3002	0.2005		
Length (m)	Mean	95.03	93.70	78.38	2.554^{ns}	1.933^{ns}
	S.D.	38.834	45.446	28.435		
Width (m)	Mean	43.17	43.44	37.62	2.369^{ns}	$<1^{ns}$
	S.D.	23.386	24.004	15.595		

1. F-max test for equality of variances among years (df = 3,26)

2. ANOVA for testing equality of means among years (df = 2,87)

TABLE 7

SIZE COMPARISON OF MULTI-USED AND SINGLE-USED RED-THROATED LOON NEST PONDS - McCONNELL RIVER, N.W.T.

		Ponds used in 3 years	Ponds used in 2 years	Ponds used in 1 year	F-max[1]	F-anova[2]
No. of Nest Ponds		5	13	49		
Area (ha)	Mean	0.256	0.375	0.314	9.60^{ns}	$<1^{ns}$
	S.D.	0.1025	0.2825	0.3175	(df = 3,4)	
Length (m)	Mean	108.60	89.30	81.63	1.45^{ns}	1.184^{ns}
	S.D.	34.370	33.532	40.443	(df = 3,12)	
Width (m)	Mean	35.40	48.92	38.79	1.659^{ns}	1.448^{ns}
	S.D.	19.256	24.669	19.155	(df = 3,12)	

1. F-max test for equality of variances among years.

2. ANOVA for testing equality of means among years (df = 2,64).

Red-throated Loon nests.

If the Red-throated Loons selected some feature of the three parameters of area, length, and width then the dimensions of nest ponds would differ from those of non-nest ponds. If the used and unused ponds have the same dimensions then it can be assumed that the nest ponds are merely a random sample of the available ponds with respect to pond size.

Table 8 indicates that nest ponds were in fact a random sample of all available ponds on the study area. There were no differences in area, length, or width between the used and un-used ponds. It appears that there was a surplus of suitable ponds on the main study area.

The smallest nest pond was 0.074 ha. The shortest was 34 m and the narrowest was 15 m. The largest nest pond was 1.46 ha and only three others were greater than 0.8 ha in area. There were only five ponds over 0.8 ha which were not used by either Arctic or Red-throated Loons. The question is, would Red-throated Loons use more of the larger ponds if there were no Arctic Loons present? In other words, are Red-throated Loons being actively excluded by Arctic Loons from the large ponds at the McConnell River? The following section attempts to answer these questions.

I.2.A.ii) Pond Size at Harrington Harbour

At Harrington Harbour there were no Arctic Loons. Thus, it was possible to examine nest pond selection by the Red-throated Loon in the absence of its chief potential

TABLE 8

COMPARISON OF SIZE OF PONDS USED FOR NESTS BY RED-THROATED LOONS WITH PONDS NOT USED FOR NESTS, McCONNELL RIVER, N.W.T.

		Nest Ponds	Non-nest Ponds	Variance[1] (F)	Mean[2] (t)
No. of Ponds		67	113		
Area (ha)	Mean	0.319	0.295	1.437^{ns}	0.632^{ns}
	S.D.	0.2709	0.2259	(df = 66,112)	
Length (m)	Mean	85.13	82.12	1.047^{ns}	0.508^{ns}
	S.D.	38.985	38.097	(df = 66,112)	
Width (m)	Mean	40.51	46.30	1.414^{ns}	1.637^{ns}
	S.D.	20.447	24.315	(df = 112,66)	

1. Variance ratio to test equality of 2 sample variances (F is two-tailed).

2. T-test for samples with equal variances (df = 178).

competitor. The much larger Common Loon (Gavia immer) was present in small numbers but no nests were found.

Eleven study areas were examined and the shores of every pond were searched for active and destroyed nests. The sizes of the ponds were determined from aerial photographs. The eleven study areas (figure 5) consisted of 3 mainland areas and 8 offshore islands. These islands ranged in size from 10.5 to 579.25 ha and contained from 4 to 33 ponds. The islands were very rugged, rocky and treeless. The 3 mainland areas, which were less rugged and contained some patches of Black Spruce (Picea mariana), ranged from 31 to 142 ha and contained from 20 to 41 ponds.

Two hundred and eighteen of the 243 visited ponds were considered suitable (i.e. size and available nest sites) for use by loons. The 25 unsuitable ponds were rejected because they lacked possible nest sites due to steep banks or thick growth of low willows which was impenetrable to loons.

A pond of 0.8 ha was considered potentially large enough for Arctic Loons based on 3 years of data from the McConnell River where 7 of 94 nest attempts were on ponds of less than 0.8 ha but 15 (15.9%) attempts were on ponds between 0.8 and 1.0 ha. Table 9 examines whether Red-throated Loons used a higher proportion of ponds over 0.8 ha at Harrington Harbour.

There was no difference in the proportion of large and small ponds used for nests ($\chi^2 = 2.05$; df = 1; P is NS).

TABLE 9

COMPARISON OF POND SIZE AND POND USE BY RED-THROATED LOONS AT HARRINGTON HARBOUR, FOR PONDS OF 2 SIZES (ABOVE AND BELOW 0.8 HA)

Size of ponds	Number of ponds		Totals
	with nests	without nests	
Under 0.80 ha	68	129	197
Over 0.80 ha	4	17	21
Totals	72	146	218

It appeared that Red-throated Loons did not select the larger ponds (over 0.8 ha) but rather they utilized a random sample of available ponds.

The four nest ponds over 0.8 ha ranged from 0.83 to only 1.125 ha. At Harrington Harbour 4 of 72 nest ponds were between 0.8 and 1.46 ha compared with 5 of 90 nest ponds at the McConnell River. These ratios were exactly the same ($\chi^2 = 0.0$). At the McConnell River there were 35 ponds between 0.8 and 1.46 ha and fully 26 of these were used by Arctic Loons and were unavailable to Red-throated Loons. Five of the remaining 9 ponds were used by Red-throated Loons.

All ponds over 1.46 ha at the McConnell River main study area were used by Arctic Loons. At Harrington Harbour there were 10 ponds over 1.46 ha. Table 10 compares the rate of usage of ponds above and below 1.46 ha. The data indicate that Red-throated Loons were avoiding the larger ponds ($\chi^2 = 5.21$; df = 1; $P<0.05$). The drawback to these data is the fact that only 2 of the larger ponds were on the off-shore islands where the density of breeding loons was highest (section III-2). The other 8 ponds were on the low density mainland study areas. However, the fact remains that none of the larger ponds was used for nesting.

The minimum pond size used at Harrington Harbour was 0.01 ha (15m X 10m) and the maximum was 1.125 ha. There were

TABLE 10

COMPARISON OF POND SIZE AND POND USE BY RED-THROATED LOONS AT HARRINGTON HARBOUR FOR PONDS OF 2 SIZES (ABOVE AND BELOW 1.46 HA)

Size of ponds	Number of ponds		
	with nests	without nests	Totals
Under 1.46 ha	72	136	208
Over 1.46 ha	0	10	10
Totals	72	146	218

7 nest ponds of 0.01 to 0.015 ha in area. These very small ponds were on the smaller offshore islands and were exposed to winds off the Gulf of St. Lawrence. These small island ponds ranged from 15 to 30 m above sea level and were subjected to almost constant breezes which provided added lift which allowed Red-throated Loons to use smaller than usual ponds.

There were landscape differences between the offshore islands and the mainland study areas and this resulted in differences in the ponds available for loons. The ponds on the mainland were significantly more variable and larger than those on the offshore islands (table 11). The two areas will be considered separately when determining whether Red-throated Loons were selecting ponds of a certain size within the acceptable range of 0.01 to 1.46 ha.

The data for used and unused ponds on the offshore island study areas are presented in table 12. If the two groups show no differences then Red-throated Loons were not selecting any particular size factor within the acceptable range. This is what occurred. There were no differences in the size or variability of any of the three measurements. The loons were using a random sample of the available ponds.

On the mainland study areas the loons were nesting on a sample of ponds which were larger, longer and wider than the unused ponds (table 13). The sample size was only 4 nests but it still yielded statistically significant differences.

TABLE 11

COMPARISON OF POND AREAS ON MAINLAND AND OFFSHORE ISLAND STUDY AREAS AT HARRINGTON HARBOUR[1]

	Mainland areas	Offshore areas	Variance[2] (F)	Mean[3] (t)
No. of ponds	90	117		
Mean area (ha)	0.266	0.144	2.109***	3.640**
S.D.	0.2719	0.1872		

** P<0.01, *** P<0.001

1. Only ponds between 0.01 and 1.46 ha are considered.
2. F test for equality of two sample variances (F is two-tailed) (df = 89,116).
3. T-test for equality of means with unequal variances (Snedecor and Cochran 1967: 114).

TABLE 12

COMPARISON OF USED AND UNUSED PONDS ON OFFSHORE ISLAND AREAS AT HARRINGTON HARBOUR[1]

		Ponds with nests	Ponds without nests	Variance[2] (F)	Mean[3] (t)
No. of ponds		68	49		
Area (ha)	Mean	0.154	0.129	1.358^{ns}	0.724^{ns}
	S.D.	0.1989	0.1707		
Length (m)	Mean	53.89	48.89	1.185^{ns}	0.873^{ns}
	S.D.	31.595	29.029		
Width (m)	Mean	29.93	25.73	1.091^{ns}	1.094^{ns}
	S.D.	20.811	19.922		

1. Only ponds between 0.01 and 1.46 ha are considered.
2. F test for equality of two sample variances (F is two-tailed) (df = 67,48)
3. T-test for equality of two means with equal variances (df = 115).

TABLE 13

COMPARISON OF USED AND UNUSED PONDS ON MAINLAND STUDY AREAS AT HARRINGTON HARBOUR[1]

		Ponds with nests	Ponds without nests	Variance[2] (F)	Mean[3] (t)
No. of ponds		4	86		
Area (ha)	Mean	0.686	0.248	1.708^{ns}	3.281**
	S.D.	0.3373	0.2580		
Length (m)	Mean	121.75	69.61	1.505^{ns}	2.230*
	S.D.	55.608	45.325		
Width (m)	Mean	67.50	35.58	1.946^{ns}	2.744**
	S.D.	31.225	22.381		

* $P<0.05$, ** $P<0.01$

1. Only ponds between 0.01 and 1.46 ha are considered.
2. F test for equality of two sample variances (two-tailed) (df = 3,85).
3. T-test for equality of means of samples with equal variance (df = 88).

Why did Red-throated Loons use larger ponds on the mainland but not on the offshore islands? A possible explanation is that none of the ponds on the offshore study areas contained any islands, whereas several of the mainland ponds did contain islands. Three of the 4 mainland nests were on islands and perhaps the loons were selecting islands rather than pond size. To test this hypothesis the area of all mainland ponds with islands was compared for those used and those not used (table 14). Red-throated Loons used the largest ponds which had islands. It is conceivable that the loons were selecting the larger ponds because the islands were surrounded by more water than islands on small ponds. Thus, the islands on the larger ponds would provide more protection from predators.

The offshore area nest ponds at Harrington Harbour were smaller than the nest ponds at the McConnell River. However, in both areas the birds were randomly selecting from the available ponds and the observed differences in size merely reflect differences in the available ponds. A comparison of ponds on the mainland study areas at Harrington Harbour with those at the McConnell River not used by Arctic Loons revealed that there was no difference in average pond size ($t = 1.09$; $df = 268$; P is NS) but Red-throated Loons used larger nest ponds at the Harrington Harbour mainland areas ($t = 2.60$; $df = 69$; $P<0.02$) in the absence of Arctic Loons.

TABLE 14

COMPARISON OF USED AND UNUSED PONDS WHICH CONTAIN ISLANDS - MAINLAND PONDS AT HARRINGTON HARBOUR[1]

		Ponds with nests	Ponds without nests	Variance[2] (F)	Mean[3] (t)
No. of ponds		3	16		
Area (ha)	Mean	0.690	0.197	2.390[ns]	2.722**
	Range	(0.0225-1.0125)	(0.0225-1.0125)		
	S.D.	0.413	0.267		

** P<0.02

1. Only ponds between 0.01 and 1.46 ha considered.
2. F test for equality of two variances (df = 2,15).
3. T-test for equality of means (df = 17).

There were only 4 ponds over 0.8 ha on the island study areas at Harrington Harbour. Two of these (1.125 and 0.83) were used for nests whereas the other two were very large (11.47 and 17.77 ha) and were not used. It was not possible to determine whether Red-throated Loons would have used more ponds in the range 0.8 to 1.46 ha on the island study areas, if they had been available.

Red-throated Loons at Harrington Harbour exhibited only a mild tendency to use larger ponds in the absence of Arctic Loons. They did not use a higher proportion of ponds over 0.8 ha at Harrington Harbour nor did they use any ponds over 1.46 ha. On the high density offshore areas they selected a random sample of available ponds (in terms of size) and only on the mainland did they utilize larger ponds. This latter use was probably an anti-predator reaction rather than expansion of pond size selection resulting from lack of competition with Arctic Loons. This suggests that Red-throated Loons at the McConnell River were restricted to the small ponds primarily by habitat selection rather than by competition with Arctic Loons.

1.2.B. Shoreline and Nest Sites

The effect of shoreline on selection of nest ponds is ultimately similar for both Red-throated and Arctic Loons. Shores which are steep, rocky, or covered with thick, shrubby vegetation are unsuitable for nests. Among shorelines which

are used for nests there are degrees of suitability. The various substrates are discussed in the next section.

i) Nest substrate - quality

The shorelines of Red-throated Loon nest ponds at the McConnell River were classified into four broad categories. These are the same classes as used for Arctic Loon ponds except that points of land are not included, as Red-throated Loon ponds were so small that they rarely had shores with points. A new category, called 'marsh islands', was added for this species. It combined the categories of islands and wet grassy and was a wet grassy area with dry islands contained in it. 'Marsh islands' were surrounded by areas of shallow water with emergent vegetation as opposed to regular islands which were surrounded by deeper, open water.

The number of nest ponds with each type of substrate was compared with the number of nests on a particular substrate (table 15). It is obvious that islands and 'marsh islands' were highly selected with 89.6% of nest ponds with each type of substrate having nests on that substrate. There were 49 ponds containing wet grassy areas and 24 (48.9%) of them had nests on this substrate. Twenty-six of the ponds with wet grassy also contained islands and 'marsh islands'. Fully 22 (84.6%) of these 26 nest ponds had nests on islands or 'marsh islands' indicating that these two substrates were preferred over the wet grassy substrate. Dry shore was least preferred with only 17 nests on it in the 80 nest

TABLE 15

SELECTION OF NEST SUBSTRATE BY RED-THROATED LOONS AT McCONNELL RIVER[1]

Substrate type and number of nest ponds with this substrate		Number of ponds with nests on							
		Dry shore		Island		Marsh island		Wet grassy	
		N	(%)	N	(%)	N	(%)	N	(%)
Dry shore	- 80	17	(21.2)	24	(30.0)	21	(26.3)	18	(22.5)
Island	- 29	0	(-)	26	(89.6)	2	(6.9)	1	(3.4)
Marsh island	- 29	1	(3.4)	0	(-)	26	(89.6)	2	(6.9)
Wer grassy	- 49	3	(6.1)	9	(18.4)	13	(26.5)	24	(48.9)

1. Based on 93 nesting attempts.

ponds which contained this habitat. Thirteen of these 17 nests were on ponds in which the only suitable substrate was dry shoreline. Red-throated Loons prefer to nest on islands and 'marsh islands' followed by wet grassy areas and lastly by dry shoreline.

When Red-throated Loons nested in wet grassy areas they built up a nest in the shallow water and were really using 'loon-made islands' with the same potential safety from mammalian predators as natural 'marsh islands'. There were 80 nest ponds with potential for island nest sites (i.e. islands, 'marsh islands' and wet grassy areas). Seventy-six (95%) of the nests on these ponds were on island-type nest bases. Islands were highly selected components of Red-throated Loon nesting ponds. However, islands were not essential as indicated by the 17 nests on dry shoreline. This is corroborated by the following analysis of nest ponds in which nests were located on islands or 'marsh islands'.

Red-throated Loons nested on islands in 19 different ponds. If all 19 ponds had been used in all three years then there would have been 57 (3 X 19) nests on ponds with islands. In fact, there were only 26 nests on these ponds. The ratio of use was 45.6% (26 of 57).

Similarly 18 different ponds with 'marsh islands' were used for nests. This would yield a maximum of 54 (3 X 18) nests if all ponds were used in each year. Actually only 26 nests were on 'marsh islands' or a ratio of pond use of 48.15%

(26 of 54). Therefore Red-throated Loons were using less than half of the ponds containing their preferred nest substrate. This does not even include any of the 113 ponds which were not used for nests. Some of these ponds also contained islands and 'marsh islands'.

Thus Red-throated Loons had a hierarchy of preferred nest sites but these did not limit the ponds used at the McConnell River. The main criterion was that at least one area of suitable nest substrate was available even if it was a less preferred substrate. This raises the question of whether there was a minimum amount of suitable substrate which was required for a pond to be used for nesting.

ii) Nest substrate - quantity

On the McConnell River main study area most ponds have their entire shorelines suitable for nests. It was not possible to test for minimum requirements in this area. The situation was different in the rockier and more rugged terrain of the Harrington Harbour region where many ponds were unsuitable and large sections of other ponds had shores which were too steep or too rocky to hold a nest. All nests at Harrington Harbour were on dry shore or islands. There were no wet grassy areas or marsh islands. Hence the potential nest sites were qualitatively similar. This makes the Harrington Harbour area a good one for illustrating any quantitative component to nest site selection.

When the ponds at Harrington Harbour were searched for nests I estimated the amount of shoreline suitable for nests. The estimates were made in per cent of shore which could hold a nest (excluding level areas of bedrock). These were strictly visual evaluations based on complete searches of pond shorelines. Some shores on the offshore islands could not be estimated due to lack of time. These appraisals, if biased, were probably biased evenly between used and unused ponds. All ponds over 1.46 ha were ignored as they were too large for Red-throated Loons (section I.2.A).

The percentage of suitable shoreline was compared for used and unused ponds (table 16). The mainland and offshore island ponds were again analyzed separately to avoid potential differences due to terrain. Only ponds with at least one structurally suitable nest site were included.

There was no difference in the amount of suitable shoreline in used and unused ponds within the limits of the sampling method. The data indicate that Red-throated Loons selected a random sample of ponds based on amount of suitable shoreline.

Another way of looking at the data is to examine whether loons nested equally on ponds with very little suitable substrate and those with substantial suitable shore. Table 17 compares pond use for ponds with 10% or less suitable shore and ponds with over 10% suitable. There is no selection for ponds with more than 10% of shoreline suitable for nests. It appears that loons require only enough shoreline for a

TABLE 16

PERCENTAGE OF SHORELINE SUITABLE FOR RED-THROATED LOON NESTS AT HARRINGTON HARBOUR[1]

Location	Ponds with nests	Ponds without nests
Offshore islands	N = 59 Mean = 59.8%	N = 40 Mean = 54.6%
Mainland	N = 4 Mean = 65.0%	N = 86 Mean = 70.5%

1. Only ponds between 0.01 and 1.46 ha are included.

TABLE 17

COMPARISON OF POND-USE FOR PONDS GROUPED BY AMOUNT OF SUITABLE NEST SUBSTRATE AVAILABLE FOR RED-THROATED LOONS - HARRINGTON HARBOUR

Study area	Percent of shore suitable for nests	Number of ponds with nests	Number of ponds without nests	Totals	χ^2[1]
Offshore islands	≤10	6	9	15	
	>10	53	31	84	
	Totals	59	40	99	2.81^{ns}
Mainland	≤10	0	8	8	
	>10	4	78	82	
	Totals	4	86	90	0.408^{ns}
Combined Areas	≤10	6	17	23	
	>10	57	109	166	
	Totals	63	126	189	0.619^{ns}

1. χ^2 with 1 df for a 2 X 2 contingency table.

nest and as long as this is present further suitable shore is unnecessary.

iii) Nest construction

Red-throated Loons (and Arctic Loons) construct two rather different types of nests. In the one case the pair use a low flat area on which they build a rudimentary nest (called a depression type nest). This is basically a hollow surrounded by small amounts of wet vegetation pulled from the nearby water. This type of nest requires very little time to construct and the loons can lay eggs in it, a few hours after building starts. As incubation progresses the sitting adults may add vegetation to the rim areas of the nest, especially after a changeover when the sitter is settling on the eggs.

The other type of nest (called built-up type nest) involves a more complex series of behaviour patterns in that a pair select a site which is usually under several centimetres of water. They then build up a substantial nest of aquatic vegetation and bottom mud. Many of these nests must be started many hours before the first egg is laid. The time of construction is probably much longer since loons are relatively inefficient nest-builders, often picking up material and throwing it away from the nest area. The largest nest measured in 1967 was 60 cm in diameter at the base and 20 cm above the water level. Nests of this magnitude must

require several days to construct. Actual figures are unavailable because all Red-throated Loon nests observed from the towers were of the simpler 'depression-type'.

A 'built-up' nest involves a high energy output by a nesting pair. It also delays the start of egg-laying by at least one and possibly two days. In arctic environments there is presumably selection for factors reducing the length of the nesting period in order to have the young fledge before freeze-up in the fall. Loons wait for water levels to reach normal before starting to construct nests (Lehtonen 1965; this study). This means that time is lost when they spend a long time actually building the nest. It seems likely that if a pair of loons spend this extra time then some counter-selective advantage must accrue to them.

How many nests of each type were constructed and under what habitat circumstances? The total number of nests of each type was the same (46:47) but the distribution by nest substrate was not (table 18). In wet grassy areas, all nests were 'built-up', by definition of the habitat as an area covered with a few centimetres of water. In the remaining three categories the loons could use either 'depression' or 'built-up' type of nests. Forty-seven of the nests in these three categories were 'depression' and 22 were 'built-up'. There was a significantly higher number of 'depression' nests when each nest-type was possible ($\chi^2 = 8.348$; df = 1; $P<0.005$ with χ^2 adjusted for continuity). This was a minimum

TABLE 18

ANALYSIS OF NEST TYPE IN RELATION TO NEST SUBSTRATE FOR RED-THROATED LOONS AT THE McCONNELL RIVER

Nest type	Nest substrate				Totals
	Dry shore	Island	Island in wet grassy	Wet grassy	
Built-up	4	5	13	24	46
Depression	13	21	13	-	47

ratio as some of the 22 'built-up' nests may have been necessitated because they were built on very low, wet land. In any event, loons chose the 'depression' type nest when a choice was possible. This is reasonable considering the extra time and energy required for the 'built-up' type of nest. This raises the question of why loons nest in wet grassy areas in view of the extra time and energy involved?

There were 43 nest ponds in which both 'wet grassy' and dry shore areas were available for nests. In these ponds 3 nests were on dry shore and 24 in 'wet grassy' areas. The rest were on islands. Red-throated Loons chose the 'built-up' nests in wet grassy areas when given this choice ($\chi^2 = 14.814$; df = 1; $P<0.005$ with χ^2 adjusted for continuity for the H_o; 24:3 = 1:1). In wet grassy areas loons spent the time and energy constructing 'built-up' nests rather than using the simpler 'depression-type' nests on the dry shores. Selection seems to have favoured the use of 'loon-made' islands. Apparently safety from predation is more important than an extra day or two spent nest-building.

Huxley (1923) mentions the use of copulation platforms by Red-throated Loons in Spitsbergen. No platforms were used by Red-throated or Arctic Loons at the McConnell River.

iv) Nest site fidelity

There were 90 Red-throated Loon nests in three years

on the main study area at the McConnell River. These nests involved 67 different ponds and it appears there is not much fidelity to ponds, much less to nest sites. There were only 18 ponds used in more than one year (table 19).

These data incidate a low fidelity to nest sites in ponds which were reused. In all 90 nest attempts a total of 79 different sites were used and only 9 were reused with one being used 3 times and 8 being used twice. Nest sites do not appear to be in short supply in this breeding area.

I.2.C. Other Factors

A variety of other factors affect a pond's suitability for use by Red-throated Loons. These are discussed below. Some of these factors also affect Arctic Loons and were discussed in more detail in section I.1.C.

i) Pond depth and escape behaviour of young Red-throated Loons

Pond depth has three components. A maximum, a minimum and a modal or most common depth. This last is the effective depth of the pond and is most important to loons, as small areas of a pond which are very shallow or very deep cannot be used by loons.

Red-throated Loons nested on small ponds and the adults generally flushed when threatened (Appendix 2). The flightless chick dived when frightened and swam along the bottom stirring up the mud with its feet. It then turned back into the muddy water and was lost from sight until it popped up for

TABLE 19

FIDELITY TO NEST SITE BY RED-THROATED LOONS

AT THE McCONNELL RIVER, N.W.T.

	No. of ponds	Number of ponds with		
		Same nest site in 3 years	Same nest site in 2 years	Different nest site in all years
Ponds used in 3 years	5	1	1	3
Ponds used in 2 years	13	-	7	6

air and then immediately dove again. It stayed in the muddy water and constantly stirred-up more sediment. The pond was soon completely murky and the loon chick was then able to hide along the shore, under an overhanging bank, or in aquatic vegetation. This behaviour was very effective against humans who were wading after the chicks and was probably useful in evading natural predators such as foxes, wolves (Canis lupis), Herring Gulls (Larus argentatus) and Snowy Owls (Nyctea scandiaca). In every case where I pursued Red-throated Loon chicks (over 35 ponds) they resorted to this type of escape behaviour.

In a deep pond, a chick would be unable to reach the bottom and stir it up. The water would remain clear and the chick would be visible as it approached the surface. A hovering predator could follow the chick's progress and capture it when it surfaced.

It is not known what the comparative probabilities of chick survival are for deep and shallow ponds. Some nest ponds at Harrington Harbour were deeper than the deepest nest pond at the McConnell River but detailed comparisons were not possible due to lack of time. The question is hypothetical at the McConnell River as all ponds were quite shallow. In fact, it seems likely that smallness and shallowness are correlated for ponds and this may account for the evolution of this type of escape behaviour in the Red-throated Loons.

There is a minimum modal depth which is acceptable to Red-throated Loons. A sample of 20 nest ponds in 1967 had an average modal depth of 39 cm with a range of 26 to 71 cm. Eight nest ponds had a modal depth of 26 to 33 cm which appears to be the minimal depth suitable for Red-throated Loons. Shallower ponds tended to become choked with vegetation later in the season.

It is not known whether there was a maximum acceptable depth for Red-throated Loon nest ponds.

ii) Bottom type

The texture and colour of the pond bottom may affect the chick's ability to escape predation. These factors will have little effect on the adults since no natural predator is likely to take a healthy adult on the nest pond.

The colour of the bottom has a potential effect on the conspicuousness of the dark gray chick swimming under water but the chick's behaviour when diving (previous section) overcomes it.

The texture of the bottom substrate is important to the escape behaviour of the chicks. There must be a layer of loose sediment on the bottom, which the chick can stir-up when swimming along it. All ponds at the McConnell River main study area have this type of soft bottom and were suitable except the two rocky ponds which were unsuitable because of lack of nest sites.

iii) Food supply

Red-throated Loons at the McConnell River did not feed on the nest ponds. They gathered all food from other areas and thus food supply on the nest territory was not a factor in habitat selection for this species. However, proximity to a food source was an important consideration in a pond's suitability (section III).

Red-throated Loons brought the following species of fish to their young: Capelin (Mallotus villosus), Slender Eelblenny (Lumpenus fabricii), Sand Launce (Ammodytes dubius), Arctic Char (Salvelinus alpinus), Greyling, and unidentified sculpin sp. (Cottidae).

iv) Visibility from pond

Visibility from nest ponds has the same effects on Arctic and Red-throated Loons and was discussed in section I.1.C.

It is evident that visibility per se was not limiting to Red-throated Loons at the McConnell River since the area is so flat. At Harrington Harbour many loons nested on ponds surrounded by low trees and hills which limited their vision. However, in all cases there was at least several metres of open ground surrounding the nest. It is probable that factors which inhibited visibility were limiting to loons through their effect on shoreline for nests (i.e. steep banks) or restricting take-off area by increasing the height which the loon must reach to avoid hitting solid objects such as steep

banks, trees, and hills.

1.3. COMPARISON OF ARCTIC AND RED-THROATED LOON NEST PONDS

It is apparent from preceding sections that pond size was the critical factor differentiating nest ponds of Red-throated and Arctic Loons. The two species had similar preferences with respect to shoreline, pond depth, bottom type, water clarity, and visibility and none of these factors limited the suitability of a pond for loon nesting. Both species preferred 'island-type' nest sites but they readily used other sites as long as at least one potential site was available. Food supply had to be nearby (within several km) but not necessarily in the nest ponds.

All nest ponds of the two species at the McConnell River main study area are compared in table 20. It was evident that Red-throated Loon nest ponds were significantly less variable in area than Arctic Loon nest ponds. Red-throated Loons were more restricted in the size of nest ponds which they used. These ponds were also significantly smaller than the nest ponds used by Arctic Loons.

I.3.A. Structural and Behavioural Correlates to Nest Pond Size

Are the two species differentially adapted (either in structure or behaviour) to the two pond sizes?

The Red-throated Loon can take off directly from water without the running start necessary for all other Loons (Bent 1919; Dement'ev et al. 1968). In fact Red-throated Loons can

TABLE 20

COMPARISON OF SIZE OF ARCTIC AND RED-THROATED LOON NEST PONDS AT THE McCONNELL RIVER (1967-68-69)

	Arctic Loons	Red-throated Loons
Number of ponds	46	67
Mean size (ha)	2.223	0.319
S.D.	2.1557	0.2709
F^1	63.31*** with df = 45,66	
t^2	5.96***	

*** P<0.001

1. F ratio to test equality of two sample variances (two-tailed).
2. Approximate t-test for samples with unequal variances.

take off from land, if pressed (this study). They normally make a short run across the water before taking flight. The run is usually 15-40 m (Norberg and Norberg 1971). This ability to make short take-offs was the principal adaptation which made the small ponds available to Red-throated Loons but not Arctic Loons which required a longer water area for take-off. These differences in take-off ability are structurally based according to Snyder (1957) but he gave no details. Norberg and Norberg (1971) analyzed the aerodynamics of the take-off and landing phases of Red-throated Loon flight but there is no similar study of Arctic Loon flight.

The comparative structure of Arctic and Red-throated Loons is examined in table 21 where data from the literature are presented. The data come from specimens from the North American breeding ranges of the two species. It was apparent that both species were about the same in all respects except for weight, where the Arctic Loon was markedly larger. The Red-throated Loon carried substantially less weight on a body only slightly smaller than that of the Arctic Loon. This may explain the increased aerial manoeuverability of Red-throated Loons. The added weight of Arctic Loons would increase their diving efficiency by reducing the bird's buoyancy. Storer (1960) has reviewed conditions favouring underwater locomotion by birds. The situation for Arctic and Red-throated Loons was illustrated by an incident during

TABLE 21

MEASUREMENTS OF ARCTIC AND RED-THROATED LOONS

(NUMBER OF SPECIMENS IN BRACKETS - IF KNOWN)

	Arctic Loon		Red-throated Loon		Ratio of Red-throated/ Arctic Loon		Source
	M	F	M	F	M	F	
Total length (cm)	58-69		66		-		1
Body Length (cm)	36-43		36-38		-		2
Flat wing (mm)	297.7 (31)	293.0 (31)	283.0 (25)	272.3 (27)	0.95	0.93	3,4,5,6,7
Culmen (mm) (exposed)	52.9 (14)	50.6 (13)	52.6 (13)	51.1 (11)	0.99	1.01	3,4,8
Tarsus (mm)	75.0 (34)	72.0 (31)	73.7 (29)	69.4 (33)	0.98	0.96	3,4,5,8
Weight (g)	2349 (5)	2115 (7)	1852 (11)	1610 (10)	0.79	0.76	4,5,6,8,9,10

1. Snyder 1957 (no sex differentiation); 2. Witherby et al. 1943 (no sex differentiation); 3. Palmer 1962; 4. Parmalee et al. 1967; 5. Manning et al. 1956; 6. Manning and Macpherson 1961; 7. Parmalee and MacDonald 1960; 8. This study; 9. Macpherson and McLaren 1959; 10. Macpherson and Manning 1959.

which single birds of each species met on a pond located between their active nest ponds. Half of the meeting pond was shallow (less than 50 cm) and the Red-throated Loon chased the Arctic Loon in this area as both half flew and half swam across the water surface. When they reached the deeper (about 1 m) section of the pond the Arctic Loon was able to dive and immediately became the pursuer. The Arctic Loon was more effective in the deeper water whereas the Red-throated Loon was more manoeuverable and dominated in the shallow water.

The different flying abilities and nest pond sizes might combine to produce behavioural differences. This was tested by examining the escape reactions of adult loons when their nest ponds were visited by a potential mammalian predator (man). The data and analysis are presented in Appendix 2 where it is shown that the two species did have different escape behaviour. These differences applied only when nest ponds were between 0.5 and 1.0 ha. Both species flew when threatened on small ponds (under 0.5 ha) which were too small for effective escape by diving or hiding low in the water. Ponds over 1.0 ha were large enough that adults of both species could easily outswim any predators or hide from them. On the intermediate sized ponds (0.5 to 1.0 ha) Red-throated Loons flew when threatened whereas Arctic Loons mainly stayed on the ponds, usually hiding in the water with only the bill exposed. Arctic Loons were more likely to

fly from these intermediate ponds than from the larger ponds (over 1.0 ha) but were even more likely to flush from the smaller ponds (under 0.5 ha). The intermediate ponds were transitional in terms of escape behaviour with Red-throated Loons utilizing their superior flying ability whereas the Arctic Loons relied on their greater underwater ability.

Differences in territorial behaviour of the two species are considered in Appendix 3 where the importance of the small size of the Red-throated Loon ponds is further emphasized.

II. ECOLOGICAL ASPECTS OF TERRITORY IN LOONS

Arctic and Red-throated Loons were strongly territorial during the breeding season. The actual territorial displays and behaviour sequences were complex and will not be discussed here as it is the results of the behaviour which are of primary interest.

The strict territoriality has implications for many facets of loon ecology. It affects the breeding dispersion, number of pairs and their success, and the interspecific division of resources. The ecological implications of loon territorial systems are analyzed in the following sections.

II.1. TERRITORY IN THE ARCTIC LOON

Each Arctic Loon territory at the McConnell River consisted of one or more ponds. These ponds were used for copulation, nesting, brooding and feeding of young, and resting and preening by the adults. They differ from Type A territory (Nice 1941; Hinde 1956) in that the adults did not feed on the territory.

The boundaries of Arctic Loon territories were usually very distinct since they coincided with the shores of the ponds making it easy to calculate the area of the territories. It was usually necessary only to determine the number and size of ponds in the territory since the land areas surrounding the ponds were not defended and were not part of the territory.

Some of the larger lakes contained more than one territorial pair. These lakes were partitioned into smaller areas by islands and points which formed the territory boundaries. Two such lakes are illustrated in figures 6a and 6b. Figure 6c outlines a large lake (8.0 ha) with no natural topographic divisions which the loons could use as boundaries. It contained only one nesting pair in each year. Loons nesting in each end of such a pond would be in constant visual contact which would probably result in high levels of aggressive interactions. It was apparent that a large expanse of open water was necessary to separate territories when no landmarks were available.

Territory boundaries using points and islands were precise. Any intrusion by one pair brought a prompt response by the residents. These interactions generally involved displays and calls which quickly re-established the integrity of the boundary.

II.1.A. Territory Stability

The boundaries of Arctic Loon territories were constant from year to year with virtually no variation. There were 35 territories which were occupied in at least one year. Thirty were used in all 3 years with 26 having nests in each year and 4 with nests in 2 years and the pair was present in the third year. Three of the remaining territories had nests in 2 of the 3 years. The other 2 had

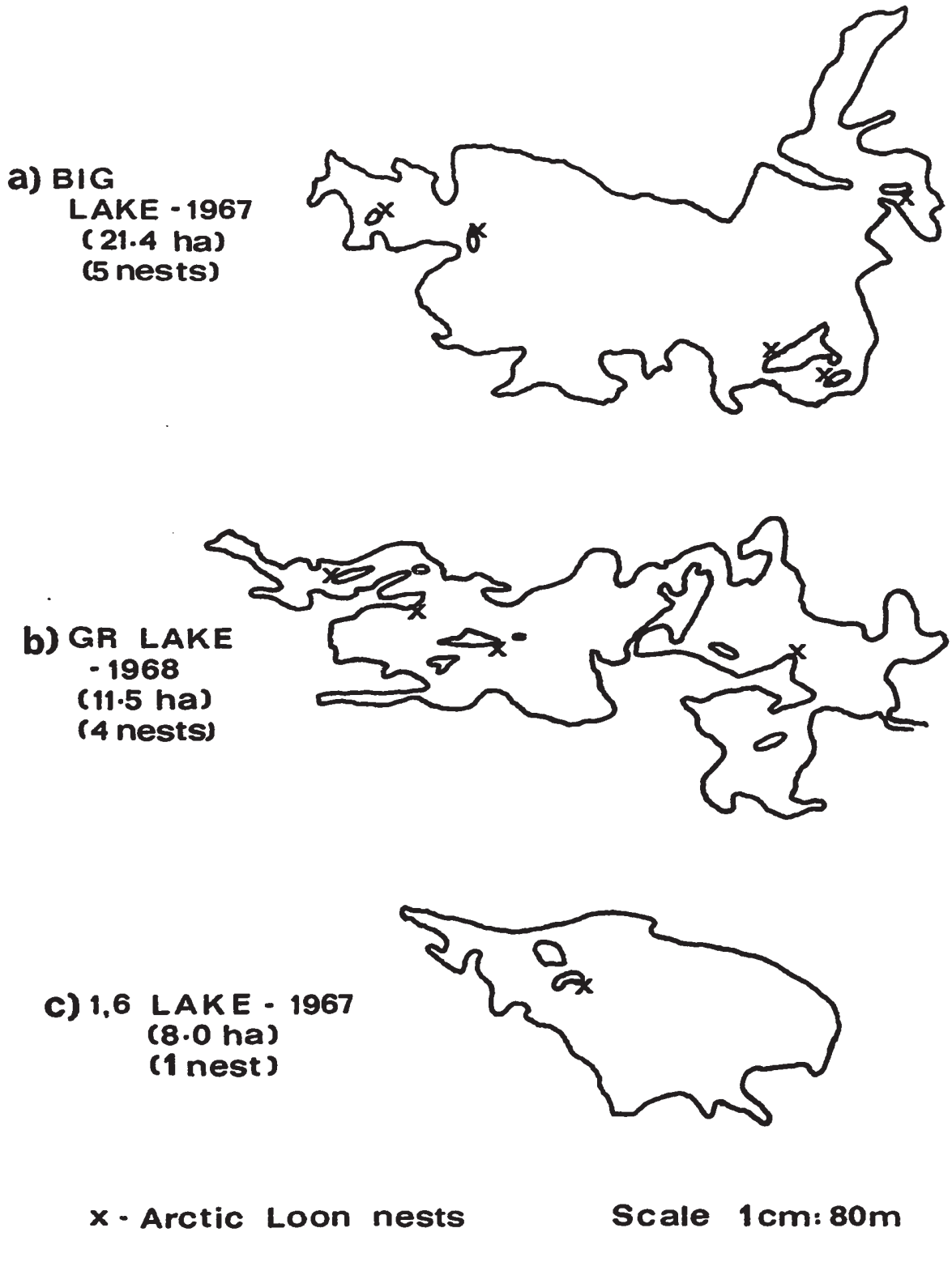

Figure 6. Location of Arctic Loon nests on typical ponds at the McConnell River. The nest locations illustrate the importance of points and islands in dividing ponds for use by several Arctic Loons.

nests in one year and a pair was present in a second year. Thus, of 35 territories, 30 were used in all 3 years and 5 were used in 2 of the 3 years. This is constant use of habitat by a bird population.

Arctic Loon territories may encompass more than one pond. This multi-use of ponds was regular from year to year for each territory. The use of the extra ponds in a territory took many forms. One pond was used for three years and the adults regularly took their young overland to a nearby pond. Several pairs nested on different ponds within the territory in two different years. They used the non-nest pond for escape, resting, and feeding of young.

There were no cases where a pond was part of a different territory in different years.

II.1.B. Size of Arctic Loon Territories

The nest ponds used by Arctic Loons varied in size between 0.225 and 9.54 ha. However, the actual territory size was less variable ranging from 1.125 to 9.54 ha. Table 22 gives the average size of all Arctic Loon territories and then partitions the territories according to the number of ponds per territory. The average territory size for all pairs was 3.66 ha. There was no difference in area of the territories with respect to the number of ponds used ($F = 0.063$; $df = 2,32$; P is NS). There was no difference in variability among the three classes of territories

TABLE 22

TERRITORY SIZE OF ARCTIC LOONS AT THE McCONNELL RIVER

	Territories with			All Territories
	One pond	Two ponds	Three ponds	
Number of territories	15	13	7	35
Mean area (ha)	3.50	3.81	3.75	3.66
Range of area (ha)	(1.125-9.54)	(1.80-9.20)	(1.30-8.82)	(1.125-9.54)
S.D.	2.623	2.228	2.546	2.398
Mean Pond area (ha)	3.50	1.91	1.25	---
Range of pond area (ha)	(1.125-9.54)	(.495-7.49)	(0.225-3.33)	---

(F-max = 1.431; df = 3,13; P is NS). This constancy of territory size suggests that Arctic Loons selected territories of a certain size regardless of the number of ponds they must utilize. This may represent the water area required to produce enough food for the young.

The number of young produced per territory was correlated with the size of the territory (r = +0.288). This correlation is close to significance (t = 1.73; df = 33; 0.10>P>0.05) and may indicate a valid trend for the number of young produced to increase with the size of the territory.

Some territories were used more than others (table 23). These data show a trend towards smaller territories being less used by Arctic Loons. The mean areas were not significantly different for the four classes (F = 0.828; df = 3,34) but the small numbers of twice-used ponds make the results inconclusive.

It is interesting to examine the smallest territories used by Arctic Loons since the average territory size is meaningless for a pair which has a smaller territory. There were only 4 territories which were less than 1.5 ha, with the smallest being 1.125 ha. This pond was used for a nest in 1967 (eggs infertile) and was occupied by a pair in 1968, which did not nest. Two territories (1.31 and 1.44 ha) each consisted of 3 small ponds with the 1.31 ha territory used for nests in 2 years and the 1.44 ha territory used for nests in 3 years. The former raised one young in 2 years and the

TABLE 23

RELATIONSHIP OF TERRITORY SIZE AND AMOUNT OF USE OF ARCTIC LOON TERRITORIES

	Territories used for 3 years		Territories used for 2 years	
	Nests in all three years	Nests in two of three years	Nests in 2 years	Nests in one of 2 years
Number of territories	25	5	3	2
Mean territory area (ha)	3.86	4.18	2.64	1.53
Range of areas (ha)	(1.44-9.54)	(1.80-8.06)	(1.31-5.26)	(1.125-1.94)
S.D.	2.412	2.772	2.273	0.573

latter raised 1 young in 3 years. The fourth small territory (1.35 ha) was used for nests in 2 years and raised only 1 young. Thus, only one of the small territories was used in all 3 years and none of them was very successful (0.33 yg/year). The average territory used for nests in all 3 years raised 2.04 young (0.68 yg/year). These ratios were significantly different ($\chi^2 = 4.21$; df = 1; $P<0.05$). It seems likely that the range of 1.125 to 1.45 ha represents the minimum acceptable territory size for Arctic Loons.

II.1.C. Density of Arctic Loon Territories

Was there room for more than the 35 territories on the main McConnell River study area? The actual number of occupied territories was 33, 34, and 33 pairs respectively in 1967, 1968, and 1969. This was virtually full use of the 35 known territories.

It is illuminating to examine loon territories and unused ponds to see if a substantial number of ponds could have been used by new pairs. A size of 1.25 ha will be considered acceptable for a complete Arctic Loon territory. There were 9 ponds over 0.75 ha which were not used by Arctic Loons (section I.1.A). Only three of these ponds were greater than 1.25 ha (1.26, 1.31, and 1.46 ha). These 3 ponds were all near the minimum acceptable pond size and were not used by Arctic Loons. They were used for nests by Red-throated Loons although they were used only 4 of a

possible 9 times in 3 years.

Would some of the ponds in Arctic Loon territories have been used by other Arctic Loons if more loons had been present? Were other Arctic Loons excluded by the territory holders? The alternative is that territory holders expand into neighbouring ponds because they are unoccupied. There were suitable extra ponds over 1.25 ha included in the territories of 5 pairs of Arctic Loons. It is unknown whether an additional pair could have used one of these ponds or whether it would have been excluded by the territory holder since no strange pair was seen to land on any of these ponds. It is known that in some territories Arctic Loons defended more than one pond. One pair nested on one pond (0.81 ha) and defended another larger pond (1.06 ha). In other cases the pairs used more than one pond and since strange birds were not seen to land on the extra ponds, no defense was necessary. In all years several instances of single birds or pairs landing on occupied territories were recorded and the presumed intruders were evicted.

The combination of stable numbers and defense of more than one pond indicate that the Arctic Loon population is at or near the maximum level possible, at the McConnell River. Territorial behaviour appears to limit the number of breeding pairs in this part of the population but the crucial question is whether a surplus of potential breeders exists. It is not possible to be sure with an unmarked population. How-

ever, any birds unable to breed in the study area have several other nearby areas to use. These areas may be less suitable and thus they may have a lower success rate. This is discussed in section III.

II.1.D. Territorial Interactions of Arctic Loons

This section analyzes quantitative aspects of territorial behaviour in terms of the number and intensity of these interactions. This allows an estimate of the strain which territory defense places on the time (and indirectly energy) budgets of Arctic Loons. It is the cost of maintaining a territorial system.

All intraspecific interactions were recorded during 2143 hours of observation of 21 Arctic Loon territories (7 in each year). These observations were spread fairly evenly throughout the daylight period. Very little loon activity occurred between 24:00 and 06:00 hours. Interactions which involved two adults on a regularly occupied territory were considered territorial when the behaviour of one of them was noticeably aggressive. Episodes involving three or four adults were assumed to have territorial implications. A separate class of interactions involving more than four adults occurred late in the season and is discussed in appendix 1.

Analysis of interactions was based on the number of encounters, their duration, the number of intruders, and

finally the proportion of time spent in territorial defense.

i) Number of encounters

The number of intraspecific encounters involving Arctic Loons is presented in table 24 where they are grouped according to the stage of the breeding cycle during which they occurred. Only one encounter occurred in an hour of observation on any particular territory and the data are expressed as the number of hours with and without encounters and were tested accordingly. There was no apparent reason for the lack of more than one encounter during an hour of observation except for the generally low overall encounter rate.

The encounter-rate was different for the various stages of the breeding cycle ($G = 67.24$; $df = 3$; $P<0.005$). The individual stages were compared by an a posteriori Simultaneous Test Procedure (Sokal and Rohlf 1969:582). The rate of intraspecific territorial encounter was lowest during the incubation and brooding periods with each having the same rate ($G = 1.89$; P is NS). The number of intrusions was higher during the pre-laying period ($G = 30.01$; $P<0.005$) and highest on territories which had lost their eggs or young ($G = 16.72$; $P<0.005$). It is during this latter period with eggs or young lost that primary territory selection probably occurs (Appendix 1) with solidification of the boundaries occurring during the subsequent pre-laying period.

TABLE 24

NUMBER OF INTRASPECIFIC TERRITORIAL ENCOUNTERS BY ARCTIC LOONS

Stage of breeding cycle	Number of hours observed		Totals
	with encounters	without encounters	
Pre-laying	54	786	840
Incubation	13	850	863
Brood rearing	8	274	282
Eggs or young destroyed	27	131	158
Totals	102	2041	2143

ii) Intensity of encounters

The intensity of territorial defense may vary with the stage of the breeding cycle and this was tested for Arctic Loons. A convenient measure of intensity was the duration of each encounter since episodes were terminated by a resident diving towards an intruder and surfacing under it. The intruding loon flew before the resident actually surfaced drom the dive.

The data on duration of encounters are presented in table 25 and are restricted to occupied territories. The variability of encounter-lengths was not equal for the three stages of the breeding cycle (F-max. = 15.99; df = 3,6; $P<0.01$). Therefore, an approximate test was necessary to compare the equality of mean encounter-lengths (Sokal and Rohlf 1969:372). This test revealed that the length of intraspecific encounters varied with the stage of the breeding cycle (F^1 = 8.48; df = 2,23; $P<0.005$). Arctic Loons became progressively less tolerant of intraspecific intruders as the breeding cycle advanced.

iii) Number of intruders

The number of intruders in each encounter varied with the stage of the breeding cycle (Table 26). The pattern of territory intrusion changed with the breeding season. Encounters during the pre-laying and incubation periods primarily involved single intruders and there was no differ-

TABLE 25

DURATION OF TERRITORIAL ENCOUNTERS AT OCCUPIED ARCTIC LOON TERRITORIES

Stage of breeding cycle	Total number of encounters	Number of encounters used[1]	Average duration of encounters (minutes	S.D.	Range (minutes)
Pre-laying	54	30	10.01	7.645	1 - 30
Incubation	13	11	7.09	5.517	3 - 22
Brood-rearing	8	7	3.71	1.912	1.5 - 7

1. Only encounters with full data are included.

TABLE 26

NUMBER OF INTRUDERS DURING TERRITORIAL ENCOUNTERS - ARCTIC LOONS[1]

Stage of breeding cycle	Number of intruders		
	Two	One	Total
Pre-laying	5	35	40
Incubation	0	13	13
Brood-rearing	4	4	8
Total	9	52	61

1. Only encounters with complete details about the number of intruders are included.

ence between the two periods ($\chi^2 = 1.79$; df = 1; P is NS). Intrusions during the brood rearing period involved two intruders more often than during the earlier stages ($\chi^2 = 9.09$; df = 1; $P<0.005$ for the H_o; 5:48 = 4:4). This increase in the number of cases with two intruders occurred at a time when several pairs had lost their nests. The single birds found in earlier stages may have been unpaired.

iv) Proportion of time spent in territorial defense

It has been shown that territorial encounters were more frequent and were longer during the pre-laying period than during later periods. The number of encounters and their length were combined and compared with the number of hours of observation to reveal the amount of time actually spent in territory defense.

Arctic Loons spent 0.18 per cent of their time in territorial defense during the incubation and brood-rearing periods and 1.07 per cent during the pre-laying period. These figures refer to the total time budget of the species except for the night period of 24:00 to 06:00. They spent 1.58 per cent of their time on territory actually defending it, during the pre-laying period. There was no difference in the rates for the other stages since at least one adult was always present during the incubation and brood-rearing periods.

In Arctic Loon territories which adjoined over open water it was necessary to defend this boundary against intrusions by swimming neighbours in addition to defending against aerial intruders. Three sets of adjoining territories were observed for a total of 97 hours during the pre-laying period (one set in each year). The pairs spent an average of 2.18 per cent of their time in mutual territorial defense and the amount was remarkably similar for the three cases (2.02, 2.25, and 2.27 per cent).

These figures refer only to the time when both adjoining pairs were present simultaneously. However, both pairs were present 73.8 per cent of the time that at least one of the ponds was occupied during the pre-laying period. Now assume that each pair was present for one half of the 26.2 per cent of the time that only one pair was present. Thus, 1.88 per cent of the time spent on territory was devoted to defense of mutual boundaries and 1.28 per cent of the total time was so spent.

It is apparent that Arctic Loons with adjoining territories spent twice as much time defending their territories as did loons which used whole ponds with no common territory boundaries. In terms of time spent on the territory, those pairs with no common boundaries spent 1.58 per cent of their time in territorial defense as opposed to 3.46 per cent (1.58 + 1.88) for pairs with such boundaries. The comparable figures for the overall time budget were 1.07 per cent and

2.35 per cent of time spent in territorial defense. Territorial behaviour was not a very time-consuming activity and was not a major drain on the time budget of Arctic Loons.

II.2. TERRITORY IN THE RED-THROATED LOON

Breeding Red-throated Loons defended a territory which consisted of a nest pond and usually one or more neighbouring ponds. These territories were used for copulation, nesting, and brood rearing but not food gathering (Type B of Hinde 1956). The nearby ponds were used for escape, resting, preening, and in some cases brood rearing. They formed an integral part of the territory and were defended against intruders.

Observations from the tower indicated that defense against intruders was very effective. If strange Red-throated Loons circled over an occupied territory the resident birds threatened them with loud calls and visual displays. These threats were often sufficient to deter the potential intruders from landing on the pond. If they did land then a bout of mutual displaying usually ensued. The bout ended when the intruders flew and only the residents remained.

On rare occasions an intruding loon or pair of loons landed on the escape pond belonging to the territory of another pair of Red-throated Loons. This caused the non-incubating member of the resident pair to fly into the

escape pond and chase the intruders away with vigorous displays. A single brooding bird would leave its young to evict intruders from a nearby pond but a lone incubating bird would not leave its eggs. The number of ponds used by a pair of Red-throated Loons was variable and is examined in section II.2.B.

II.2.A. Territory Structure

The number of ponds used by Red-throated Loons was determined by observing the escape behaviour of adults during my routine nest visits. Adults flushed from the nest ponds as I approached. They either landed on a nearby pond or circled overhead while I was at the nest pond. Escape ponds used under these circumstances were considered part of the territory of the pair. The validity of this assumption was checked by comparing observations from the tower on seven undisturbed pairs with the results from visits to these seven nests. Pairs used the same rest and escape ponds when undisturbed as they did when flushed by humans. The two methods were in complete agreement indicating that results from nest visits gave a reliable estimate of the ponds actually used by a pair.

The non-nest ponds used in these territories were very similar in characteristics to the actual nest ponds. In fact, many of the non-nest ponds in one year had been used for nests in a previous year.

The total water area in a Red-throated Loon territory was not as important as the number of ponds in the territory. If Red-throated Loons were selecting territories of a certain size then there should be no correlation between area of a territory and the number of ponds in the territory. This was the case with Arctic Loons (II.1.B). To test this hypothesis for Red-throated Loons the territory size of each pair was correlated with the number of ponds in that territory. The correlation coefficient was 0.624 which is highly significantly different from zero ($t = 4.587$; $df = 33$; $P<0.001$). This correlation suggests that Red-throated Loons were selecting the number of ponds in a territory and that territory size was not important in itself.

Territory structure was very stable in this species. The same sets of ponds were used every year. There were no cases in which a pond was part of one territory in one year and part of a different territory in another year. There were two cases of the same pond being used by two or more pairs. In both cases the ponds were either the third or fourth ponds (in terms of use) in the territories of the birds concerned. This may have been a function of the visit technique occasionally forcing birds onto abnormal ponds. Both of these ponds were quite large (1.17 ha and .405 ha).

There were 39 territories on the main study area. The number of ponds in each of these territories is presented in table 27. Four was the maximum number of ponds used in

TABLE 27

NUMBER OF PONDS PER RED-THROATED LOON TERRITORY FOR DIFFERENT SECTIONS OF THE MAIN STUDY AREA AT THE McCONNELL RIVER

Section of study area (see Fig. 2)	Number of territories with				Mean number of ponds per territory
	One pond	Two ponds	Three ponds	Four ponds	
A	1	5	2	3	2.64
B	0	1	5	4	3.30
C	2	2	2	3	2.67
D	0	3	1	2	2.83
Totals	3	11	10	12	2.86

Does not include the three territories on the periphery of the main study area.

a single season by a pair. Four territories contained five ponds each over the three year period. However, in any one year, they consisted of only four ponds.

In most territories the component ponds were adjacent to each other but this was not always the case. One territory in 1968 consisted of three ponds whose location formed a triangle. The sides of the triangle (distance between ponds) were 820 m, 550 m and 410 m. There was another active nest pond within this hypothetical triangle.

Most territories consisted of contiguous ponds which tended to buffer the nesting pairs from each other. This may have reduced antagonistic interactions between pairs but it was not a necessary condition for nesting. In the High Beach study area several territories were actually adjoining with territory boundaries centred on islands and points.

Most pairs used two or more ponds for their territories but three pairs were each restricted to a single pond (2 of the 3 verified by observations from towers). When these single pond territories were visited the adults circled overhead until the observer left the area. If more than a few minutes were spent at these nest ponds then the adults usually disappeared, presumably landing in Hudson Bay or the McConnell River. The adults were then out of sight of their nest ponds. This behaviour seems less adaptive than having a suitable escape pond where the adults could land, in

sight of their nest ponds. An adult which has flushed because a mammal is in the area leaves its eggs or young vulnerable to attack by gulls and jaegers. If the adult is on a nearby escape pond it can see the aerial predator and return to the nest pond to chase the predator. The presence of escape ponds is advantageous in an area where mammalian predators are present such as the McConnell River. It would be less important in areas such as the small offshore islands in the Harrington Harbour area where there are no regular mammalian predators.

Table 27 shows that Red-throated Loons use the same number of ponds per territory in all sections of the study area ($F = 0.958$; $df = 3,32$; P is NS). This number ranges from 2.64 to 3.30 ponds per territory. This regularity between areas is interesting in view of the large differences in the number of available ponds in each section. The number of ponds not used for territories (by either loon species) was one in section A, 9 in B, 28 in C, and 37 in D. Thus the Red-throated Loons did not use more ponds when a surplus was available such as in the inland areas. By the same reasoning it appears that territory size was not compressed in the heavily used section A. It will be shown in section III that it is advantageous for Red-throated Loons to nest as close to the Hudson Bay coast as possible in order to be nearer their food source. It would then seem advantageous for loons nesting in area D which is 14 km from the coast to nest in Area A which is only 9 km from the coast. Since

they do not use Area A it is concluded that area A will not support any more Red-throated Loon territories because of the territorial behaviour of the established pairs.

II.2.B. Number of Red-throated Loon Territories

There were 39 distinct Red-throated Loon territories on the main study area at the McConnell River. This includes 3 territories on the periphery of the study area. The use of the 39 territories is detailed below

Total number of territories	= 39
Number with nests in 3 years	= 23
Number with nests in 2 years and a pair present in the third year	= 7
Number with nests in 2 years	= 6
Number with nest in one year and a pair in the second	= 1
Number with nest in one year only	= 2

Thirty territories were used in all three years, 7 in two years, and only 2 were used just once. This is a high degree of territorial reuse considering that only 32 territories were occupied in 1968.

There were 37 territories used in 1967 and 1969 compared with the 32 used in 1968. The drop in territory holders in 1968 was correlated with severe spring flood conditions and a corresponding delay in the availability of the breeding ponds. Some of the territories classified as unoccupied in

1968 may have had resident pairs which, when breeding was not undertaken, rarely occupied the territories. The delayed season and the flood conditions caused nest visits to be undertaken later in the season and this may have resulted in some occupied territories being classed as unoccupied. Thus the 1968 total of occupied territories should be considered a minimum figure.

Red-throated Loons had very stable territories in terms of the ponds used in successive years. The actual pond used for the nest often changed from year to year. Table 28 examines all territories in which the actual nest pond was known in at least two years. It is evident that there is much changing of nest ponds within territories.

Is this lack of fidelity to nest ponds related to nest success in the previous season? It seems reasonable to assume that a pair will reuse a pond if it has been successful there. Nest site fidelity has been correlated with nest success in Yellow-eyed Penguins (Megadyptes antipodes) (Richdale 1957:81), Skylarks (Alauda arvensis) (Delius 1965) and Prairie Warblers (Dendroica discolor) (Nolan 1966). Tree Swallows (Iridoprocne bicolor) which raised young were more likely to return to the same area than were unsuccessful birds (Bradstreet 1969).

Choice of a nest pond was related to nest success in the previous year (table 29). The loons were more likely to change ponds if their nest attempt in the previous year had

TABLE 28

RE-USE OF NEST PONDS BY RED-THROATED LOONS AT THE McCONNELL RIVER

Territories with	Number of territories with nests on			Total number of territories
	Same pond in all 3 years	Same pond in 2 years	Different pond in all years	
Nests in 3 years	6	11	5	22
Nests in 2 years	-	5	8	13

TABLE 29

RELATIONSHIP OF NEST POND FIDELITY TO NEST SUCCESS IN PREVIOUS YEAR FOR RED-THROATED LOONS AT THE McCONNELL RIVER

Outcome of nest	Pond used in next year		Totals
	Same pond	Different pond	
All eggs lost	5	15	20
All young lost	7	4	11
At least one young raised	10	9	19
Totals	22	28	50

been unsuccessful. These differences are very close to significance levels ($\chi^2 = 5.226$; df = 2; $0.1>P>0.05$ for the H_o; 5:15 = 7:4 = 10:9).

An examination of the nests which lost all their young reveals that the 7 pairs which used the same pond in the next year, lost their last young at an average age of 6.4 days whereas those that changed ponds lost their last young at an average age of 8.5 days. These averages are not significantly different (t = 0.92; df = 9; P is NS).

A reasonable hypothesis is that a pair of loons is more likely to re-use a pond upon which it has expended much energy such as feeding young. The hatching of eggs represents a threshold in the energy regime of an adult loon. The parent must transfer from a relatively easy existence during incubation, when much time is spent loafing, to a strenuous regime of fishing and of feeding young which are several kilometres from the food source. With this background it is valid to group the pairs which raised young with those that lost young and compare them with pairs which lost their eggs; in other words, a comparison of pairs abandoning their nest attempts before and after the threshold event of the eggs hatching. Among those pairs which lost their young, the average age at loss of the last young was 7.1 days. Pairs of Red-throated Loons which lost their eggs were more likely to change to a new pond in the next breeding season than were pairs which were able to raise

their young for at least a few days ($\chi^2 = 4.88$; df = 1; $P<0.05$ for the H_o; 5:15 = 17:13).

Territories were examined for a relationship between the number of ponds in a territory and the nest success in that territory. Does the presence of extra ponds in a territory have survival value for Red-throated Loons?

Table 30 shows a trend of higher success being correlated with a larger number of ponds per territory. These differences are not statistically significant ($F = 1.18$; $df = 3,85$; P is NS with data transformed by the square root of $X + \frac{1}{2}$) (Steel and Torrie 1960:157). This was due to the small number of nest attempts in territories with only one pond. The very fact that there were so few attempts on one-pond territories indicates that Red-throated Loons using territories with more than one pond were selectively favoured.

II.2.C. Territorial Interactions of Red-throated Loons

Intraspecific territorial encounters were analyzed quantitatively to assess the amount of time used in territorial defense and the effect of the stage of the breeding cycle on this amount. The analysis is based on 1253 hours of observations at 12 Red-throated Loon territories.

i) Number of encounters

The number of encounters was examined by the same method used for Arctic Loons (i.e. number of hours with and

TABLE 30

RELATIONSHIP BETWEEN THE NUMBER OF PONDS PER RED-THROATED LOON TERRITORY AND NEST SUCCESS[1]

Number of ponds per territory	Number of territories	Number of nest attempts	Number of young raised	Number of young/nest attempts
1	3	7	1	0.14
2	10	19	7	0.37
3	13	33	18	0.55
4	12	30	14	0.47
Totals	38	89	40	0.45

1. Only nest attempts with known outcomes are considered.

without encounters). The data appear in table 31 and reveal that differences in the rate of territorial intrusions varied with the stage of the breeding cycle ($G = 24.71$; $df = 3$; $P<0.005$). The individual breeding stages were compared by an a posteriori Simultaneous Test Procedure (Sokal and Rohlf 1969:582). The rate of intrusion was lowest during the incubation period ($G = 9.49$; $P<0.025$). There were no differences during the other three stages.

However, during the brood rearing period, both adults were occasionally simultaneously absent from the territory and this increased the chances of intruders landing on these ponds. This occurred in 5 of the 12 cases of intrusion. When these cases were omitted the intrusion rate was lower during the brood-rearing period than in the pre-laying and destroyed nest phases ($\chi^2 = 6.06$; $df = 1$; $P<0.025$ for the H_o; 7:310 = 28:449). The rate was the same for incubation and brood-rearing periods ($\chi^2 = 3.49$; $df = 1$; $P<0.1$ for the H_o; 7:310 = 3:451). This agrees with the results obtained for Arctic Loons.

ii) Intensity of encounters

The length of an intraspecific territorial encounter depended on the strength of the aggressive responses of the residents. The data on duration of encounters are presented in table 32 for those episodes whose length was known. The data for the incubation period were not sufficient to test

TABLE 31

NUMBER OF INTRASPECIFIC TERRITORIAL ENCOUNTERS

BY RED-THROATED LOONS

Stage of breeding cycle	Number of hours observed		Total
	with encounters	without encounters	
Pre-laying	20	370	390
Incubation	3	451	454
Brood-rearing	12	310	322
Eggs or young destroyed	8	79	87
Totals	43	1210	1253

TABLE 32

DURATION OF TERRITORIAL ENCOUNTERS AT RED-THROATED LOON TERRITORIES

Stage of breeding cycle	Total number of encounters	Number of encounters used[1]	Average duration of encounters (minutes)	S.D.	Range (minutes)
Pre-laying	20	17	3.43	2.189	0.5 - 10
Incubation	3	2	2.50	2.121	1 - 4
Brood-rearing[2]	10	10	1.75	1.419	0.5 - 5

1. Encounters of known duration

2. Includes 3 cases where intruders landed when the residents were absent. The encounter began when a resident returned.

and only the pre-laying and brooding periods were compared.

The variability of encounter-length was equal for the pre-laying and brood-rearing periods ($F = 2.38$; $df = 17,10$; P is NS) but the mean length was greater during the pre-laying period than during the brood-rearing period ($t = 2.16$; $df = 25$; $P<0.05$). Red-throated Loons which had young evicted intruders faster than did loons which had not yet laid eggs.

iii) Number of intruders

The number of intruders in each encounter was the same during the pre-laying and brood-rearing periods ($\chi^2 = 0.937$; $df = 1$; P is NS for the H_o; 15:5 = 9:1 which is the ratio of encounters with one intruder to those with two intruders, during the pre-laying and brood-rearing stages respectively). Only two encounters were observed during the incubation period (both of which had only one intruder). The overall totals were 26 encounters with one intruder and 7 with two intruders.

iv) Proportion of time spent in territorial defense

The amount of time Red-throated Loons required for territorial defense is examined by the same method which was used for Arctic Loons. Red-throated Loons spent 0.29 per cent of their total time in territorial defense during the pre-laying period. The corresponding figures for incubation and brood-rearing periods respectively were 0.03 per cent and 0.11 per cent.

When the data were restricted to times during which the birds were actually on the territory, they spent 0.46 per cent of their time in territorial defense during the pre-laying period, 0.03 per cent during incubation, and 0.17 per cent during brood-rearing.

Territorial defense was not a major drain on the time budget of the Red-throated Loon.

III. BREEDING DISTRIBUTION OF LOONS

III.1. BREEDING DISTRIBUTION AT THE McCONNELL RIVER

The four peripheral study or survey areas (figure 2) were searched for loon nests in order to compare distribution patterns in these areas with patterns on the main study area. The primary survey method was to search the areas for adult loons. When a loon was seen, that pond was searched for a nest. This method was very effective when used by an experienced observer because there was always at least one adult on an active nest pond which had not been disturbed. Since the survey areas were so flat it was possible to examine a pond for loons while still over a kilometer away from it. Thus, the loons were not disturbed and were still on the nest ponds. When a nest was found its location was marked on an aerial photograph.

Each pond was classified in the field on the basis of depth, shoreline, and visibility. Ponds which were too shallow or had unsuitable shoreline (no nest sites) were rejected from further consideration. Less than one per cent of the ponds were so rejected. Visibility was unlimited from all ponds. The area, length and width of all ponds were measured from aerial photographs.

Ponds were then classified on the basis of area as to whether they were suitable for Arctic or Red-throated

Loons. Any pond over 0.1 ha and under 0.8 ha was considered a potential Red-throated Loon pond. Ponds over 0.8 ha were classified as suitable for Arctic Loons. This cut-off point is based on 3 years of nesting data from the main study area (section I.2.A). It was impossible to examine territory size as opposed to pond size in the survey areas because of shortage of time. Thus, the basic unit of comparison is pond size and any pond not actually used for a nest is placed in the unused category even though it may have been part of a loon territory.

The overall survey data are summarized in table 33 and are analyzed in the following sections.

III.1.A. Density of Breeding Arctic Loons

The method of Snedecor and Cochran (1967:247) was used to test for a linear trend in proportion of ponds used for nests by Arctic Loons with distance to the coast in kilometers. Using the data from all 8 survey regions in table 33 yields a regression coefficient of -0.015289 which is significantly different from zero at $P = 0.0016$ ($Z = -3.135259$). Therefore, the proportion of ponds which was used decreased as the distance from the coast increased.

It was proposed in section II.A that Arctic Loons in the main study area were using virtually all suitable ponds and no further territories could be established. If this was the case, then there should not have been a signi-

TABLE 33

NUMBER OF NESTS OF RED-THROATED AND ARCTIC LOONS IN VARIOUS AREAS NEAR THE McCONNELL RIVER, N.W.T.[1]

Location	Area surveyed (ha)	Distance[2] to coast (km)	Total number of ponds	Ratio of nest:non-nest ponds[3]	
				Arctic Loons	Red-throated Loons
Triangle L.	1134	35	29	2:14	0:13
Up-river	440	20	124	5:22	3:94
Spike	440	13	47	5:28	0:14
Main Study Area					
Section D	450	14	80	16:10	6:48
Section C	400	12	70	8:10	9:43
Section B	400	10	59	10:10	9:30
Section A	400	9	34	1:3	11:19
High Beach	352	3	39[4]	7:3	17:12

1. All areas were surveyed in 1969 except the Spike area which was done in 1967.

2. Distance from centre of survey area to low tide-line of Hudson Bay.

3. Ponds between 0.1 and 0.8 ha considered suitable for Red-Throated Loons
   Ponds over 0.8 ha considered suitable for Arctic Loons.

4. Estimated number of distinct pond sections.

ficant regression of proportion of ponds used, on distance from the coast, because there should be no differences in the five areas (including High Beach). This was the case as there was no difference in the proportion used in the 5 areas ($b = -0.005732$; $Z = -0.357557$; $P = 0.72$ and is NS). This lends support to the theory that Arctic Loons were at maximum density in the study where all unused ponds were actually parts of breeding territories.

At the McConnell River adult Arctic Loons fed exclusively at Hudson Bay. However, young Arctic Loons were fed primarily on food gathered in the nesting territory by the parents. Thus, there is probably selection favouring nesting near the coast but it does not seem too rigorous for distances up to 15 km since the adults can easily reach the coastal food sources. The low proportion of pond-use in the Spike area was partly due to the sterile nature of many of the ponds which had rocky shores and bottoms.

III.1.B. Density of Breeding Red-throated Loons

The data for pond use by Red-throated Loons were also analyzed for a linear trend in the proportion of ponds used (table 33). Testing all 8 areas gave a highly significant negative regression of proportion of ponds used, on distance from the coast ($b = -0.020766$; $Z = -6.567362$; $P<0.00001$). This method should probably not be used with low values such as the zero ponds in the Triangle Lake and

Spike areas, since the method is basically a chi-square analysis. In the binomial distribution the expected values equal the mean and in the Triangle Lake area the observed value of zero is as far from the expected value of 6.5 as possible. Strictly speaking, the method should be weighted by the mean of each sample. However, this is very tedious and unnecessary for the present case, since the results are so clear-cut. The following analysis eliminates this problem and gives very similar results.

The data were restricted to the four parts of the main study area and the High Beach area. These restricted data still yielded a highly significant negative regression of proportion of ponds used, on distance from the coast ($b = -0.044321$; $Z = -5.083850$; $P<0.0001$).

There was a steady decrease in the proportion of ponds used for nests as distance to the coast increased. However, unlike the Arctic Loons, Red-throated Loons decreased in abundance even within the main study area. This difference is related to the fact that adult Red-throated Loons feed their young with fish gathered from Hudson Bay whereas Arctic Loons feed their young on food gathered in the nesting territory. Thus, distance to the coast is a much more potent force influencing nesting distribution in the Red-throated Loon than in the Arctic Loon. The actual processes involved will be discussed in the section on the feeding of young loons (section IV).

At the High Beach area there were 17 nest ponds and only 12 non-nest ponds which would seem to be an exception to the situation on the main study area where Red-throated Loon territories usually consisted of two or more ponds. These totals refer only to ponds suitable for nesting and do not include water areas which were too large for Red-throated Loon nesting but which could be used for escape. In actual fact there were enough unused water areas to supply an escape area for every nest.

III.2. BREEDING DISTRIBUTION OF RED-THROATED LOONS AT HARRINGTON HARBOUR

The breeding distribution of Red-throated Loons was determined in July 1970 on 11 study areas near Harrington Harbour (figure 5). The purpose was to find out whether breeding distribution was governed by the same factors at Harrington Harbour as at the McConnell River.

There were 218 ponds suitable for nesting loons, 10 of which were over 1.46 ha and were too large for use by Red-throated Loons (section II-2). The following analysis examines the remaining 208 ponds and is based on table 34.

The first point is whether there was a difference in breeding density between ponds on the mainland and ponds on offshore islands? The hypothesis of equal pond-use in the two habitats is rejected ($\chi^2 = 65.27$; df = 1; $P<0.005$ for the H_o; 4:87 = 68:49). There was a much higher ratio of used to unused ponds on the offshore islands than

TABLE 34

BREEDING DISTRIBUTION OF RED-THROATED LOONS ON THE NORTH SHORE OF THE GULF OF ST. LAWRENCE

Location	Total area (ha)	Area surveyed (ha)	Distance to low tide-line[1] (km)	Number of ponds	Number of suitable[2] ponds	Ratio of used to unused ponds[3]
Lake Island	579.3	362.8	0.6	33	25	4:21
Yankee Harb.	211.7	102.2	0.5	12	12	3:9
Main Island	152.4	102.5	0.4	17	13	4:9
Large Isl. sub-total	943.4	567.5	-	62	50	11:39
East Island	101.8	101.8	0.35	12	11	8:3
Cliff Isl.	44.2	44.2	0.35	12	11	11:0
Boat Islands	79.8	79.8	0.25	24	19	15:4
Wapitigun Isl.	46.6	46.6	0.2	27	23	21:2
Netagamu Isl.	10.6	10.6	0.15	4	3	2:1
Small Isl. sub-total	283.0	283.0	-	79	67	57:10

Continued .....

TABLE 34

(CONTINUED)

Location	Total area (ha)	Area surveyed (ha)	Distance to low tide-line[1] (km)	Number of ponds	Number of suitable[2] ponds	Ratio of used to unused ponds[3]
Mainland-A	31.2	31.2	2	20	19	1:18
Mainland-B	84.5	84.5	2.7	41	38	2:36
Mainland-C	142.3	142.3	2	41	34	1:33
Mainland sub-total	258.0	258.0	-	102	91	4:87

1. Distance from centre of survey area to nearest low-tide-line.

2. Ponds less than 1.46 ha in area and with suitable shoreline.

3. Ratio of nest to non-nest ponds.

on the mainland.

Large offshore islands had a lower density of breeding Red-throated Loons than the smaller islands. The three islands which were over 150 ha were placed in one group and the other five (East, Cliff, Boat, Wapitigun and Netagamu Islands) were placed in another group, with islands less than 102 ha. There were 50 suitable ponds on the large islands and 11 were used for nests by Red-throated Loons. There were 57 nests on the 67 suitable ponds on the smaller islands. The difference in density between the two categories was pronounced ($\chi^2 = 46.79$; df = 1; $P<0.005$ for the H_o; 11:39 = 57:10).

A comparison of breeding density on large islands (11 of 50 ponds used) and the mainland (4 of 91 ponds used) revealed that these two areas also had significantly different breeding densities ($\chi^2 = 10.52$; df = 1; $P<0.005$).

The above data indicated that small islands (100 ha or less) were preferred over large islands (over 150 ha) which in turn were preferred over the mainland areas. There seem to be two possible factors influencing this distribution of breeding loons. They are location of food resources and presence of predators.

The distance of the nest pond from the sea influences the amount of food available to the young which are fed by their parents with fish from the sea. This factor was very important at the McConnell River and may partially explain

the low density on the mainland areas at Harrington Harbour, which were further from the sea than were the offshore islands. It does not explain the difference in density on the large and small islands. Islands were not very different in terms of distance of ponds from low tide-line (table 34). The maximum distance from the centre of an offshore island to the sea was 600 m on Lake Island. It is not likely that this short distance strained a parent's ability to feed a brood.

It is possible that fish have a patchy rather than a uniform distribution. This could influence the distribution of breeding loons. However, it is hard to imagine that food patches were located close to small islands but not to large islands as both sizes were interspersed at Harrington Harbour (figure 5). Food does not seem to be the important factor controlling breeding distribution at Harrington Harbour. This leaves predation as the probable operative force.

Man, predatory gulls and Red Foxes (Vulpes fulva) are the three principal predators of Red-throated Loons and their eggs and young.

There is now virtually no large scale human interference with loons (R. Jones, pers. comm.) although historically there has been substantial 'egging' in the area (Audubon 1960; N. Jones, pers. comm.).

Large breeding populations of Great Black-backed

Gulls (Larus marinus) and Herring Gulls occupied the offshore islands and were potential predators of the eggs and young of the loon. In most cases, if the loons are undisturbed by man they are capable of defending their eggs and young from attacks by these gulls. This fact was verified at the McConnell River where Herring Gulls were singularly unsuccessful at catching defended loon chicks.

It was noted that the islands with large loon populations also had the highest density of breeding sea-birds and gulls. This suggests that the same factors affected the distribution of all these species. A large percentage of the nests of these seabirds (Black Guillemot - Cepphus grylle, Razorbill - Alca torda, Common Puffin - Fratercula arctica, Common Murre - Uria aalge, and Common Eider - Somateria mollissima) and gulls would have been accessible to a marauding Red Fox.

Mammalian predation has been postulated as the selective factor favouring island over mainland nesting in several bird species (Hammond and Mann 1956; Keith 1961; Barry 1964; Norderhaug et al. 1965; Ryder 1969; Ahlen and Anderson 1970). The Red Fox has a local reputation as a predator of birds and their eggs at Harrington Harbour where the foxes reach the offshore islands on the irregular winter ice (R. Jones, pers. comm.). Once the foxes reach an island they find an abundant food supply in the summer months but the critical periods are the autumn, winter and

early spring when birds are not breeding. During this time the foxes must seek alternative food sources, presumably small mammals. The number of small mammals is proportional to the amount of suitable habitat and a large island is more likely to supply enough food for a family of foxes than is a small island.

The direct evidence for the importance of fox predation in this region is anecdotal. The only fox I saw during the surveys of the offshore islands was one on Yankee Harbour Island. It was carrying three adult Black Guillemots in its mouth. This fox had a den with pups on this large island. Foxes have often been seen on Lake Island and Yankee Harbour and were also frequent on Main Island (St. Mary's group) but in recent years have been shot by the warden of this federal sanctuary (N. Jones, pers. comm.).

The concentration of breeding sea-birds, gulls and Red-throated Loons on the small islands suggests that foxes are a critical selective force for all of these birds. It remains to explain the difference in breeding density on large islands and the mainland. This could be partly due to the proximity to the sea of the large islands. It is also probable that fox populations on the large islands are less stable than those on the mainland and the foxes place a steadier pressure on the loons which breed on the mainland. This is supported by the fact that three of the four Red-throated Loon nests on the mainland were on islands

in the nest ponds.

The distribution of Red-throated Loons was apparently governed by different factors at the McConnell River and at Harrington Harbour. The primary force at the McConnell River was distance to food supplies whereas fox predation was critical at Harrington Harbour where most pairs had equal access to food sources. At the McConnell River, loons used 'island type' nests (section I) presumably in response to Arctic Fox (Alopex lagopus) predation but overall distribution was determined by food.

Karvik (1964) found that Red-throated Loons tended to nest near good fishing waters in Sweden indicating that food strongly influenced distribution.

It appeared that Red-throated Loon territories on the small offshore islands at Harrington Harbour did not have escape ponds. Fifty-seven pairs on small islands had only 10 escape ponds to choose from (table 34). However, all of these nest ponds were less than 350 m from the low tide-line and apparently the sea was used for escape and resting. The maximum distance between escape and nest ponds at the McConnell River was 550 m. The same territory structure does apply in each area.

III.3. INTERSPECIFIC BEHAVIOUR

Strict habitat selection or interspecific competition could account for the observed differences in the use of

habitat by the two species. The role of interspecific behaviour is analyzed in this section.

When an individual of one species landed on the occupied territory of the other species the result was usually a direct confrontation which was not characterized by prolonged display. The most common action was a direct chase across the water in conjunction with high intensity displays and calls. Such encounters were potentially dangerous to the participants as these loons are capable of killing each other (Lensink 1967; Jones and Obbard 1970).

Arctic Loons on Red-throated Loon territories

In view of the large number of ponds in the study area and the interspersion of loon territories, a high incidence of interspecific territorial intrusions was expected. This was not the case as Arctic Loons were only observed to enter Red-throated Loon territories on 8 occasions (in 1253 hours). This was 0.0064 encounters per hour.

Seven of the eight cases involved single Arctic Loons while the other involved a pair. This latter pair was on a Red-throated Loon territory when the residents were absent. At least one Red-throated Loon was present during the other seven intrusions. One of these seven cases is omitted from further consideration as I flushed the birds inadvertently.

In two cases, one incubating Red-throated Loon and one intruding Arctic Loon were present. On one pond the Red-throated Loon did not leave its nest although the Arctic Loon stayed on the pond for 32 minutes and was as close as 6 feet from the nest. On the other pond the Red-throated Loon left the nest but was promptly chased onto shore by the Arctic Loon. When the Red-throated Loon left the shore it was chased back onto it by the intruder. The resident was thus stranded on shore almost 15 feet from its nest and eggs. The Arctic Loon finally left on its own initiative.

In four encounters there were two Red-throated and one Arctic Loon present (2 during pre-laying, 1 during incubation, and 1 after the nest was destroyed). The Arctic Loon was chased away in three cases including once from the pond above where the single Red-throated Loon was kept on shore by the single intruding Arctic Loon. When both members of the pair were present the Arctic Loon was evicted. The pair of Red-throated Loons flushed during the fourth encounter leaving the single Arctic Loon. This unusual case occurred 11 days before nest initiation by the Red-throated Loons and the area was still flooded.

The data suggest that one Arctic Loon dominated a single territorial Red-throated Loon but if both members of the Red-throated Loon pair were present then they dominated the single Arctic Loon. No case was observed where two Arctic and two Red-throated Loons were present at the same

time.

In the three cases where the Arctic Loons were evicted, the encounters averaged 3.3 minutes (range 2-4 minutes). The average encounter length was 15 minutes (range 6-32 minutes) for the three cases where the Arctic Loons were not chased away.

Arctic Loons were present on the territories of Red-throated Loons, 0.084 per cent of the time (63 minutes in 1253 hours).

Arctic Loons tended to land on the larger Red-throated Loon ponds. The average area of the eight ponds into which Arctic Loons intruded was 0.638 ha whereas the average Red-throated Loon nest pond size was 0.319 ha. These ponds were different in area ($t = 2.72$; $df = 73$; $P<0.01$) although the variability was the same ($F = 2.28$; $df = 7,66$; P is NS). Red-throated Loons nesting on larger ponds ran a significantly greater risk of having an Arctic Loon enter their territory.

Arctic Loons were tested to see if the presence of Red-throated Loons on territory inhibited the Arctic Loons from landing on that pond. Did Arctic Loons land equally often on Red-throated Loon territories when the residents were present and when they were absent? The data are grouped as the number of hours with and without encounters (table 35). There was no difference in the intrusion rate whether Red-throated Loons were present or absent ($\chi^2 = 0.108$; $df = 1$;

TABLE 35

COMPARISON OF RATE OF INTRUSION BY ARCTIC LOONS ONTO RED-THROATED LOON TERRITORIES WHEN RESIDENTS WERE PRESENT AND ABSENT

Arctic Loons	Number of hours when Red-throated Loons		
	on territory	not on territory	Total
Not present	1035	210	1245
Present	7	1	8
Total	1042	211	1253

P is NS). The intrusion rate per hour was 0.0067 when Red-throated Loons were present and 0.0047 when they were absent.

Red-throated Loons on Arctic Loon territories

There were 10 cases of Red-throated Loons landing on Arctic Loon ponds. This represents 4.7 encounters per thousand hours (10 in 2143 hours). Seven cases involved one Red-throated Loon, one case involved two, and two cases involved more than two Red-throated Loons. Eight of the ten encounters occurred on ponds regularly used by Arctic Loons. The other two were on ponds only occasionally used by Arctic Loons (includes the two cases when more than two Red-throated Loons were present).

Arctic Loons were present during three encounters on regularly used ponds and in a fourth the Arctic Loon returned to its pond after the Red-throated Loon had arrived. In all four cases the Red-throated Loons were quickly evicted (average = 2 minutes). All of the cases involved one Red-throated Loon and three cases had one Arctic Loon and the other had two. An Arctic Loon chased a Red-throated Loon from an occasionally used pond after nine minutes. No Arctic Loons were present during the other five intrusions and the Red-throated Loons stayed an average of 26 minutes during the four cases which were timed.

Red-throated Loons were present on Arctic Loon territories, 0.096 per cent of the time (124 minutes in

2143 hours). When the Arctic Loons were present this figure dropped to 0.015 per cent.

Red-throated Loons showed no preference for landing on a particular size of Arctic Loon pond. The average area of these ponds was 2.40 ha compared with an average 2.22 ha for all Arctic Loon nest ponds ($t = 0.227$; $df = 52$; P is NS). The variability of the two samples was the same ($F = 2.927$; $df = 45,7$; P is NS). The two ponds used only occasionally by Arctic Loons are not included.

Red-throated Loons were tested to see if the presence of Arctic Loons inhibited them from landing on that Arctic Loon pond. Table 36 demonstrates that Red-throated Loons avoided Arctic Loon ponds when the residents were present ($\chi^2 = 21.01$; $df = 1$; $P<0.005$). The number of intrusions was 0.0199 per hour when Arctic Loons were absent and only 0.0017 per hour when they were present.

Red-throated Loons avoided Arctic Loons but the Arctic Loons did not avoid Red-throated Loons and dominated them when matched equally (numerically).

The two loons maintained completely distinct interspecific territories. The tundra habitat was simple and there was no way in which the two species could coexist spatially unless they established mutually exclusive territories. Orians and Willson (1964) have pointed out the importance of structurally simple habitat in promoting interspecific territorialism.

TABLE 36

COMPARISON OF RATE OF INTRUSION BY RED-THROATED LOONS ONTO ARCTIC LOON TERRITORIES WHEN RESIDENTS WERE PRESENT AND ABSENT

Red-throated Loons	Number of hours when Arctic Loons		
	on territory	not on territory	Total
Not present	1788	345	2133
Present	3	7	10
Total	1791	352	2143

III.4. COMPARISON OF INTER AND INTRASPECIFIC TERRITORIAL BEHAVIOUR

A comparison of interspecific and intraspecific territorial behaviour provides information about the levels of aggression elicited by other loon species as opposed to conspecifics.

There were four cases of Red-throated Loons invading Arctic Loon territories when the residents were present. These were compared (by paired comparison) with four cases of intraspecific intrusions by Arctic Loons during the same stage of the breeding cycle. Thus an interspecific encounter during the pre-laying stage was compared with an intraspecific encounter of average length (i.e. 10.0 minutes for Arctic Loons) during the same period. The Red-throated Loons were evicted by Arctic Loons significantly faster than were conspecific intruders during corresponding stages of the breeding cycle ($t = 3.96$; $df = 3$; $P<0.05$). There was no difference between the length of encounters when Arctic Loons landed on Red-throated Loon ponds and intraspecific Red-throated Loon encounters ($t = 1.30$; $df = 4$; P is NS).

Thus when Red-throated Loons evicted Arctic Loons they did so at the same rate (intensity) as for conspecifics. Arctic Loons eliminated Red-throated Loons faster than they evicted conspecifics but at approximately the same rate as Red-throated Loons evicted Arctic Loons.

There were significantly more intraspecific encounters

than interspecific ones (tables 37 and 38). Arctic Loon territories were visited by intruding Arctic Loons more often than by Red-throated Loons ($\chi^2 = 77.60$; df = 1; $P<0.005$). Red-throated Loon ponds also had more conspecific intruders than Arctic Loon intruders ($\chi^2 = 24.52$; df = 1; $P<0.005$).

The amount of time spent in intraspecific territorial defense was also greater than that spent in interspecific defense. This was demonstrated by comparing the ratio of the number of minutes with and without intraspecific and interspecific encounters. Arctic Loons spent more time in intraspecific defense than defending against Red-throated Loons ($\chi^2 = 412.35$; df = 1; $P<0.005$). Red-throated Loons spent more time defending against conspecifics than against Arctic Loons ($\chi^2 = 9.90$; df = 1; $P<0.005$).

The number of interspecific trespasses by each species was tested in table 39. The number of hours with and without interspecific encounters was compared for the territory of each species. There was no difference in the number of times one species intruded onto the territory of the other species ($\chi^2 = 0.443$; df = 1; P is NS). When the resident birds were present, Red-throated Loons were less likely to intrude onto Arctic Loon territories than Arctic Loons were to intrude onto Red-throated Loon territories ($\chi^2 = 4.72$; df = 1; $P<0.05$ for the H_o; 3:2140 = 7:1246 which is the rate of the number of hours with and without encounters). The same

TABLE 37

COMPARISON OF INTERSPECIFIC AND INTRASPECIFIC TERRITORIAL INTRUSIONS ON ARCTIC LOON PONDS

Intruding species	Number of hours		Total
	with intrusions	with no intrusions	
Arctic Loon	102	2041	2143
Red-throated Loon	10	2133	2143
Total	112	4174	4286

TABLE 38

COMPARISON OF INTERSPECIFIC AND INTRASPECIFIC TERRITORIAL INTRUSIONS ON RED-THROATED LOON PONDS

Intruding species	Number of hours		Totals
	with intrusions	with no intrusions	
Arctic Loon	8	1245	1253
Red-throated Loon	43	1210	1253
Total	51	2455	2506

TABLE 39

NUMBER OF INTERSPECIFIC INTRUSIONS BY ARCTIC AND RED-THROATED LOONS

Intruding species	Number of hours		Total
	with intrusions	with no intrusions	
Red-throated Loon	10	2133	2143
Arctic Loon	8	1245	1253
Total	18	3378	3396

pattern was observed for the amount of time spent in interspecific territorial behaviour. Each species intruded onto the other's territory for the same length of time ($\chi^2 = 0.863$; df = 1; P is NS for the H_o; 124:128456 = 63:75117). When the analysis was restricted to territories upon which the residents were present then the Arctic Loons spent less time in interspecific defense than did Red-throated Loons ($\chi^2 = 45.86$; df = 1; $P<0.005$ for the H_o; 19:128561 = 58:75122).

The analysis indicated that interspecific territory was much less of a strain on the time budget of the two species than was intraspecific territory. Interspecific interactions were rare which indicates that interspecific territory was not the sole factor isolating the two species.

It is noteworthy that the loons responded at least as violently to interspecific intruders as to intraspecific ones. In fact, Arctic Loons repelled Red-throated Loons faster than they evicted conspecifics. This was clearly not a case of mistaken identity. It was highly directed aggression.

IV. GROWTH AND SURVIVAL OF YOUNG LOONS AT THE McCONNELL RIVER

In 1968 and 1969 young Red-throated Loons were periodically caught, marked and measured. The purpose was to document growth patterns, feeding rates and survival.

IV.1. BASIC GROWTH RATES

Analysis of loon growth was relevant to this study since the patterns of growth combined with parental feeding and anti-predator behaviour to place constraints on what habitat was suitable for loons.

IV.1.A. Methods

The loon chicks were captured with hand nets of the type used by sport fishermen. This method was very effective at the McConnell River where all ponds could be waded. The young loons became increasingly difficult to catch as they grew older and it was virtually impossible to catch them on large ponds. Thus, I decided to concentrate on Red-throated Loons rather than Arctic Loons.

The chicks were marked with a small amount of Testor's airplane dope on the top of the head. This method was successfully used on young Common Loons (Gavia immer) by Olsen and Marshall (1952). Care was taken to apply a thin layer and to avoid excessive matting of the feathers. When released, the chicks paid no attention to the paint. It did not affect their

behaviour or that of their parents. This was verified by observation from the towers.

Chicks were usually marked within 24 hours of hatching of the first of the two eggs. The second hatched 24 hours after the first and the age of each chick was thus known.

Three measurements were taken of each chick: weight, tarsus length, and exposed culmen length. Chicks were placed head down in a funnel made of waterproof cloth. The loon and funnel were then weighed in the field on a spring balance (Welsh Scientific Co.). All weights were accurate to within 2 or 3 per cent. The portable scales were periodically compared for accuracy with an Ohaus triple beam balance.

The linear measurements were made with dial calipers and are accurate within 1 mm. The exposed culmen measurement was taken from tip of the upper mandible to the anterior edge of the head feathers. The tarsus measurement was that described by Palmer (1962).

Forty-three known age broods of Red-throated Loons were captured, measured and released. This represented 67 young which were measured a total of 217 times.

IV.1.B. Growth Rates

The growth rates of Red-throated Loons are presented in figures 7 and 8. The data refer only to the first hatched young of broods in 1969. The reasons for this restriction will become evident in later sections.

The growth of the culmen and tarsus is basically incremental linear growth as the measurements are length of upper mandible and length of tarsal-metatarsal bones. The data were analyzed for linear regression of length on age and the equations are included in figure 7. The regression coefficient for culmen growth is 0.861 which is significantly different from zero ($F = 3207.77$; $df = 1,93$; $P<0.001$). The culmen grows at an average of 0.861 mm per day from a length of 9.944 mm at hatching.

The regression coefficient for tarsus growth is 1.690 which is also significantly different from zero ($F = 2199.78$; $df = 1,93$; $P<0.001$). The average daily tarsal growth is 1.690 mm with a length at hatching, of 26.088 mm.

The increase of weight with age is a more complicated relationship. The growth of body weight is considered to be an exponential function of multiplying cells (Huxley, 1932; Laird et al. 1965; Cock, 1966). Rather than fitting a non-linear regression to the weight data the raw data are plotted in figure 8 with weight transformed to a logarithmic scale. This transformation gives a more realistic picture of the actual rate of growth. The curve is typical of avian growth curves (Ricklefs 1968).

IV.1.C. Ecology of Differential Growth

"Rates of growth vary enormously among animals. Few grow at the maximal potential rate, but all at a rate which is

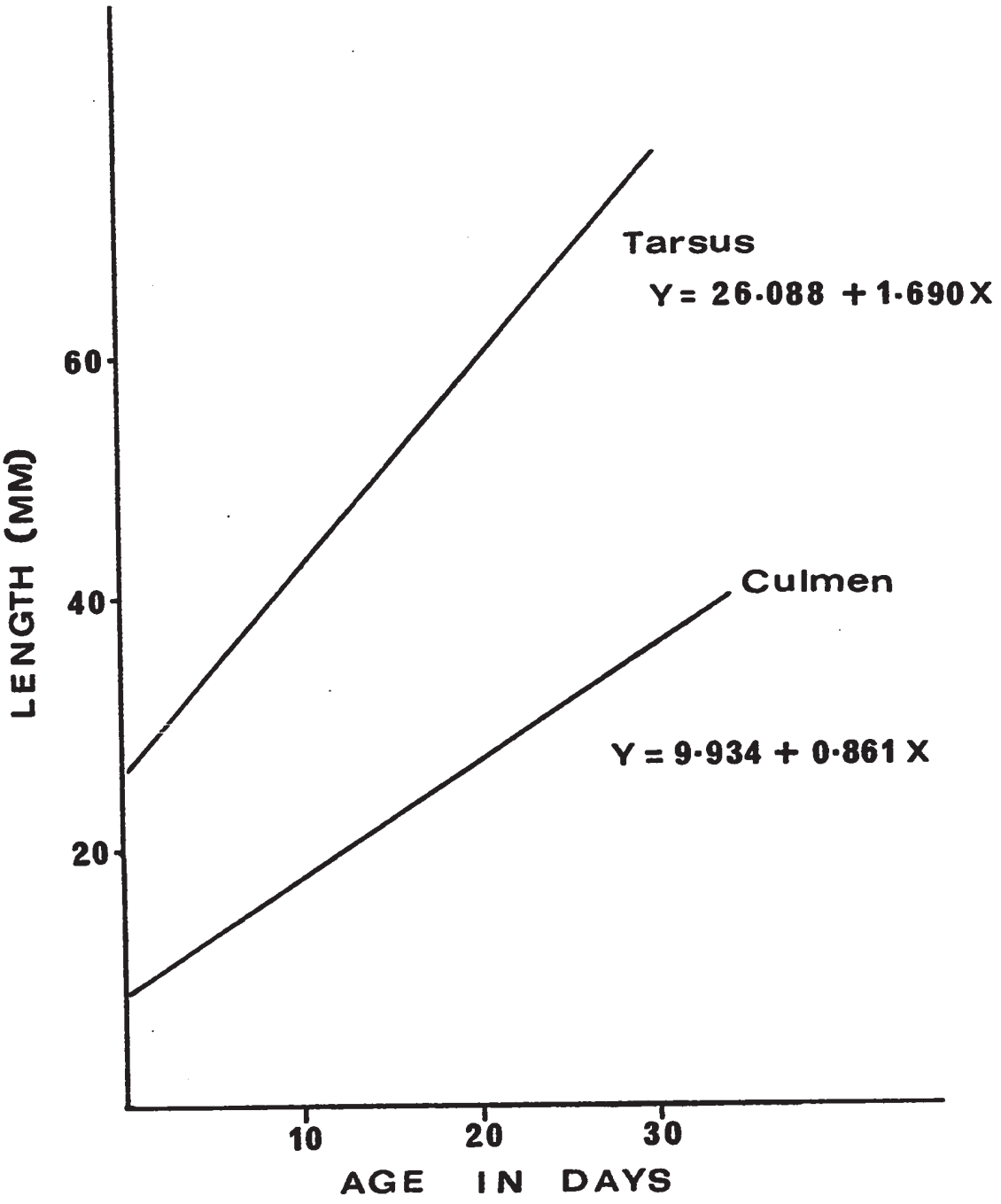

Figure 7. Regression lines for rates of growth of tarsus and culmen of Red-throated Loons in 1969 at the McConnell River. Only first hatched brood-members are included.

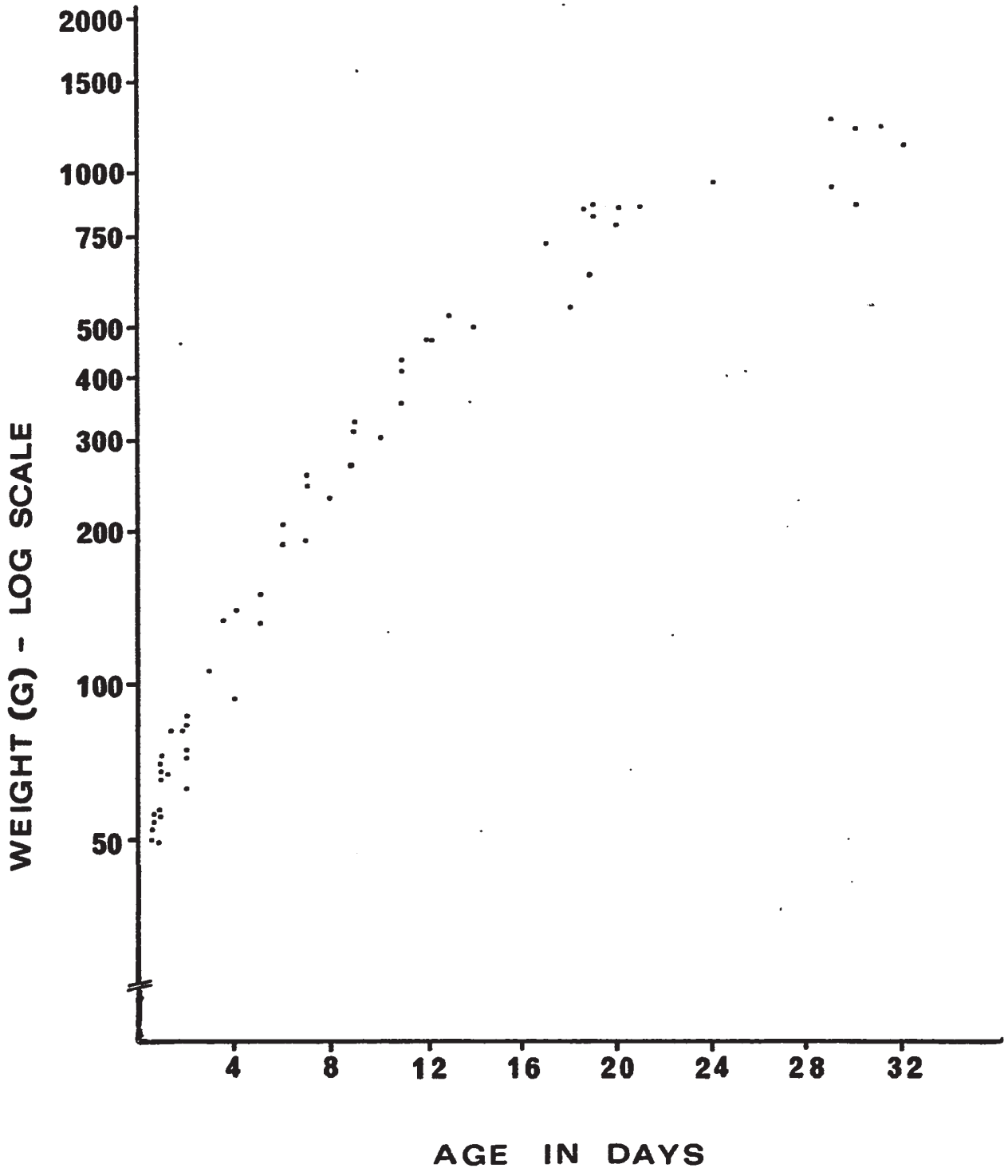

Figure 8. Weight gain by Red-throated Loon chicks at the McConnell River in 1969. Only first hatched brood-members are included.

adapted to the particular requirements of the species." (Needham, 1964). "Development rate must come under the influence of natural selection." (Ricklefs, 1969). A loon chick receives a limited amount of energy which must be apportioned to the development of various body parts. Energy is channeled into those aspects of growth which are most necessary for the chick's survival. It is not surprising then, that the actual rates of growth of the various parts of the loon body are not the same. These differential growth rates are related to the ecology of the birds during the chick stage.

It is important for a chick to become a strong swimmer (tarsus growth) as soon as possible. This proficiency would have high survival value for escape from predators. On the other hand there would not be strong selection for early growth of culmen since all food is provided by the parents for at least the first five weeks in Arctic Loons and until the young fly in Red-throated Loons. The length of the culmen does not affect the chick's ability to swallow a fish brought by the adults. The size of the gape is the limiting factor. A comparison of tarsus and culmen growth should indicate different rates of growth.

The data from figure 7 were transformed into percentages of adult measurements. An average adult culmen length of 51.85 mm and an average adult tarsus length of 71.55 mm were calculated based on 58 measurements of tarsus and 22 of culmen

taken from the literature (Manning et al, 1956; Palmer 1962; Parmalee et al, 1967). These figures are adjusted for equal values of each sex and fall between the actual average sizes of male and female Red-throated Loons in which the males are slightly larger. The transformed regression equation for culmen growth was $Y = 19.178 + 1.660X$ and for tarsus growth was $Y = 36.46 + 2.37X$. These regression coefficients are still highly significant as they are only transformed by a constant and the F values do not change.

The culmen was 19.18% of adult culmen length at hatch whereas the tarsus was 36.43% of adult tarsus length. The tarsus also grew more rapidly with an average increase of 2.37% of adult length per day while the culmen added only 1.66% of adult length per day. These two regression coefficients are highly significantly different ($t = 11.577$; $df = 186$; $P<0.001$). The regression equations can be used to predict the age at which adult lengths are reached. Red-throated Loon chicks would reach adult culmen length at approximately 49 days of age but adult tarsus length is reached at 27 days of age. It is clear that the tarsus develops more quickly than the culmen and that both increase in a steady linear manner.

Loon chicks are down-covered when they hatch. This is the stage A of Palmer (1962). A second stage (B) appears between one and two weeks (this study) in Red-throated Loons and consists of the "downlike modified terminal barbs of the as yet undeveloped juvenal feathers" (Palmer, 1962: 23). The

first juvenal feathers to appear are the primaries which first break the sheath at about two weeks of age. The next juvenal feathers are the contour feathers of the ventral surface which appear between three and four weeks.

The ecological consequences of this pattern are obvious. The primaries must grow as rapidly as possible so that the chick can fly before freeze-up. The appearance of the ventral contour feathers allows the chick to remain on water almost continuously. These juvenal feathers are more waterproof than the down stage. This is important for Red-throated Loon chicks, as both their parents may be away fishing leaving the chicks in the water hiding against the shore. In Arctic Loons it reduces the amount of time spent brooding and increases the time available for feeding on the nest pond. Both primaries and ventral feathers are selected for early appearance.

It seems that most of the early energy intake goes into growth of the body resulting in a rapid initial weight gain rather than into feather growth. This rapid increase has several advantages. It allows the chick to defend itself against gulls and jaegers at least until the parent can help. I saw a 2 week old Red-throated Loon threaten a hovering Herring Gull and keep it at bay until the adult loon (which I had frightened away) returned and the gull flew off. This episode lasted 2 or 3 minutes and at two weeks of age the young loon was big enough to cause the gull to hesitate before

attacking.

The rapid early growth allows the young to eat larger fish which it swallows whole. It is advantageous to be able to eat large fish as soon as possible. Extended observations were made on two nests of Red-throated Loons. When the brood was under one week of age only 44 of the 53 fish brought to the nest pond by the adults were eaten by the young. Forty-eight fish were brought to broods between 7 and 16 days of age and all were eaten by the young. These ratios of eaten to not eaten are significantly different ($P = 0.0021$ by Fisher's Exact test). Of the 9 fish which were not eaten by the small young, some were certainly too large for them. In some cases the young could not even lift the fish much less swallow it. Rankin (1947) noted similar behaviour by young in Scotland.

The early size increase tends toward conservation of energy by the young as the surface/weight ratio decreases as size increases and a smaller proportion of body heat is lost per unit time (Thomson 1964).

There are two counter-selective forces at work. One tends towards early growth of flight feathers whereas the other works for early increases in body size. The body weight increases are paramount for the first two weeks or so but then the primaries begin to appear and the proportion of energy devoted to body growth decreases. The growth of primary feathers and later the body feathers requires a significant energy output (Hanson 1962). Holcomb (1968) reviews several

studies (nidicolus species) which correlated decrease in weight gain with onset of feather growth.

The growth of the longest primary was measured in 1969 on Red-throated Loon chicks. The feather growth was linear and described by the regression equation $Y = -36.16 + 2.86X$ which is highly significant ($F = 299.65$; $df = 1,22$; $P<0.001$). This equation predicts that the primary first appears at the age of 12.6 or approximately 13 days. If the appearance of the primaries signifies a change in growth strategy then the rate of weight gain should decline after 13 days.

Weight gain for the period up to and including 13 days of age was compared with weight gain after 13 days. The weights were transformed to logarithms. The regression equation for the period 0-13 days if $Y = 1.71 + 0.083X$ which is a highly significant linear regression ($F = 1844.76$; $df = 1,79$; $P<0.001$). The equation for the period after 13 days is $Y = 2.52 + 0.018X$ which is also significant ($F = 60.01$; $df = 1,21$; $P<0.001$). The growth rates (regression coefficients) for the two periods are significantly different ($t = 21.54$; $df = 100$; $P<0.001$). There was a marked decrease in weight gain with the beginning of the growth of primary feathers.

The feeding behaviour of the adults was correlated with early growth patterns. One parent brought fish from the sea to the nest pond while the other stayed with the young. The first few days were spent in almost continuous brooding,

but by one week of age the young spent much time swimming or sitting on shore, not being brooded by the adult. Even though the young required little brooding, at least one parent remained with the young until they were about two-weeks old. The average age of the first young when both adults first left the nest territory simultaneously was 13 days (range 10-15; N = 7).

Table 40 compares the number of times that at least one adult was on territory when the nest was visited or observed incidentally from an observation tower. The second part of the table compares the number of minutes when no adults were present with the number when at least one was present, during continuous observations. The rate was significantly different during visits ($\chi^2 = 38.43$; df = 1; $P<0.005$) and continuous observations ($\chi^2 = 1975.92$; df = 1; $P<0.005$). Thus, the adults did not begin to leave their young until the young were about two weeks old and able to defend themselves.

IV.2. EFFECTS OF ASYNCHRONOUS HATCHING

Red-throated and Arctic Loons lay their eggs two days apart (N = 4 for Red-throated Loons and N = 5 for Arctic Loons). The eggs hatch one day apart and in a brood of two young the first hatched is a full day older than the second hatched (N = 22 for Red-throated Loons and N = 10 for Arctic Loons). The following analyses were undertaken to determine whether the broodmates differed in survival, growth, and feeding rates.

TABLE 40

RELATIONSHIP OF PARENTAL CARE TO AGE OF YOUNG

RED-THROATED LOONS

Age of oldest young (days)	Number of observations with[1]		
	at least one adult present	no adults present	Totals
0 - 12	172	3	175
13 and over	46	17	63
Totals	218	20	238

	Number of minutes with[2]		
	at least one adult present	no adults present	Totals
0 - 12	8400	57	8457
13 and over	1275	455	1730
Totals	9675	512	10187

1. Based on nest visits and non-continuous observations from the towers.

2. Based on continuous observations of active nest ponds.

It was possible that one of the two colours used to mark the young was more conspicuous than the other and caused the chick to be more susceptible to predation. Table 41 gives the number of each age group (first hatched and second hatched) which were marked with each colour. The same number of each group were marked with the respective colours ($\chi^2 = 0.189$; df = 1; P is NS).

Since each age-class was marked equally, the survival rates of birds marked with each colour was tested in table 42. It is obvious from this table that colour has no differential effect on the mortality rate ($\chi^2 = 0.013$; df = 1; P is NS).

The actual disappearance of young loons was not observed. The ever present Herring Gulls and Parasitic Jaegers constantly patrolled the area and presumably ate any small loon chicks which were unattended by parents. These predators would most likely take those young which were weakened or dead through lack of food.

IV.2.A. Differential Survival

Twenty-four Red-throated Loon broods of two chicks were analyzed (6 in 1968 and 18 in 1969) for survival of each brood member. The data (table 43) indicated a much higher survival rate for the first hatched member of a brood ($\chi^2 = 12.80$; df = 1; $P<0.005$). Only three of the second hatched young survived to three weeks old which was the deadline for acceptance in this table.

TABLE 41

NUMBER OF EACH CLASS OF YOUNG GIVEN A PARTICULAR COLOUR

(RED-THROATED LOONS, 1968-69)

Age	Number of young marked with		Totals
	Red	Yellow	
First hatched	13	11	24
Second hatched	11	12	23
Totals	24	23	47

TABLE 42

NUMBER OF CHICKS OF EACH AGE WHICH SURVIVED

(RED-THROATED LOONS, 1968-69)

Outcome	Number of young marked with		Totals
	Red	Yellow	
Survive	9	9	18
Not survive	15	14	29
Totals	24	23	47

TABLE 43

SURVIVAL OF FIRST HATCHED AND SECOND HATCHED CHICKS

(RED-THROATED LOONS - POOLED 1968-1969)

	First Hatched	Second Hatched	Total
Survive	15	3	18
Not survive	9	21	30
Total	24	24	48

There were 9 first hatched young which died. In 3 of these cases the second hatched young pre-deceased the first hatched and in 4 cases both disappeared together. In one case the second-hatched died after the first and only once did the second young survive after the first had died.

The data for marked broods of Arctic Loons are limited but they show the same trend as the Red-throated Loons. In seven marked broods all the first-hatched young survived past two weeks of age whereas only 5 of the 7 second-hatched young survived.

IV.2.B. Differential Growth

Broods of 2 were measured in 1969 and the differences in growth rates were analyzed. There were 37 measurement pairs on 16 broods when both brood members were alive. The difference between first and second hatched young was plotted against the age of the older young (figure 9). The regression lines for these differences are analyzed in table 44.

If the two young grow at the same rate then the size differences between them should not increase with age. However, it is obvious that the differences do increase with age. These differences are all highly significant and are quite large. The older chick gained an average of 20.3 g per day more than the younger chick. The tarsus of the older young increased 0.48 mm and the culmen 0.25 mm per day more than the respective figures for the second hatched young. The first hatched young grows much faster than the second

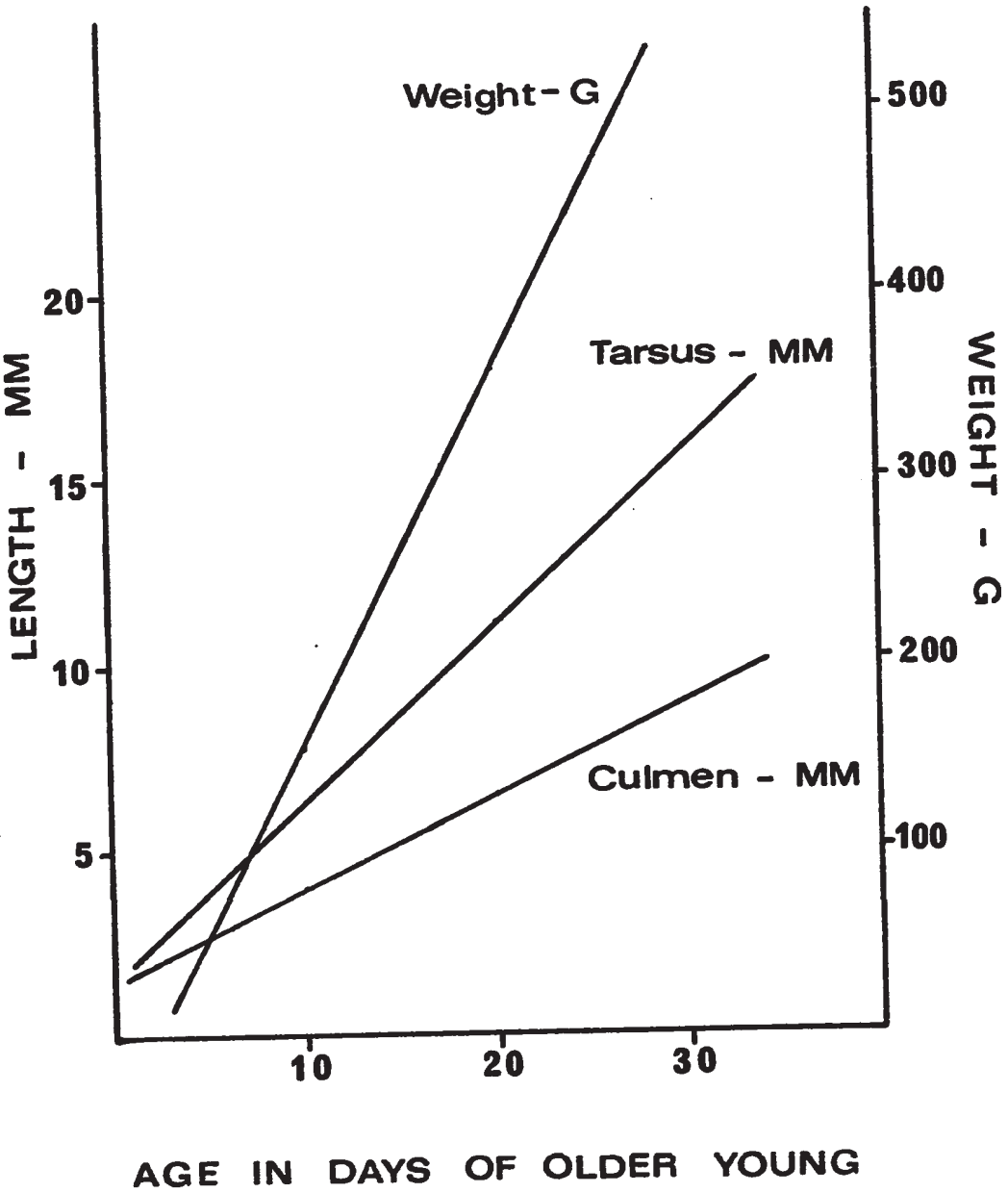

Figure 9. Differences in growth-rates of older and younger members of the same brood of Red-throated Loons at the McConnell River in 1969. Data expressed as the difference in size between brood members.

TABLE 44

ANALYSIS OF SIZE DIFFERENCES BETWEEN BROOD-MATES

(RED-THROATED LOONS)[1]

Source	Regression Coefficient	F-Value[2] for H_o: $\beta = 0$	P	Regression Coefficient as percent of adult measurement
Weight	20.3116	216.65	0.001	1.1740
Tarsus	0.4812	45.67	0.001	0.6725
Culmen	0.2486	43.76	0.001	0.4795

1. Based on 16 broods in 1969.

2. df = 1,35.

hatched young.

IV.2.C. Feeding Rates of Brood-mates

In broods of two the older chick survives better and grows faster than the younger chick. These differences were correlated with relative food intake for each brood member.

In 1969 three Red-throated Loon nests with known age broods of two were observed from towers (2) and a portable blind (1). These broods were fed fish brought to the nest ponds by their parents. The number of fish fed each young at the three nests is presented in table 45.

All three nests exhibited similar feeding ratios between first and second young ($\chi^2_{(3 \times 2)} = 0.132$; df = 2; P is NS. Since each ratio was similar it was valid to pool the data and analyze the totals for equality of feeding rates by the first and second hatched young. The first hatched young was fed significantly more fish than the second hatched young ($\chi^2 = 10.223$; df = 1; $P<0.005$ with χ^2 adjusted for continuity).

The first hatched young ate about twice as many fish as the second hatched. However, this ratio was not constant throughout the day. Early in the day the first hatched chick received a high proportion of all fish brought to the pond (figure 10). The younger chick got most of its food later in the day. It received 60% of all fish in the period from 20:00 to 24:00 hours.

The day was divided into three equal periods of 8 hours.

TABLE 45

NUMBER OF FISH EATEN BY FIRST HATCHED AND SECOND HATCHED YOUNG AT THREE RED-THROATED LOON NESTS (1969)

Nest Number	No. of hours observed	Number of fish eaten by		Totals
		First hatched	Second hatched	
1	24.25	9	5	14
2	107.85	43	20	63
3	22.00	11	6	17
Totals	154.10	63	31	94

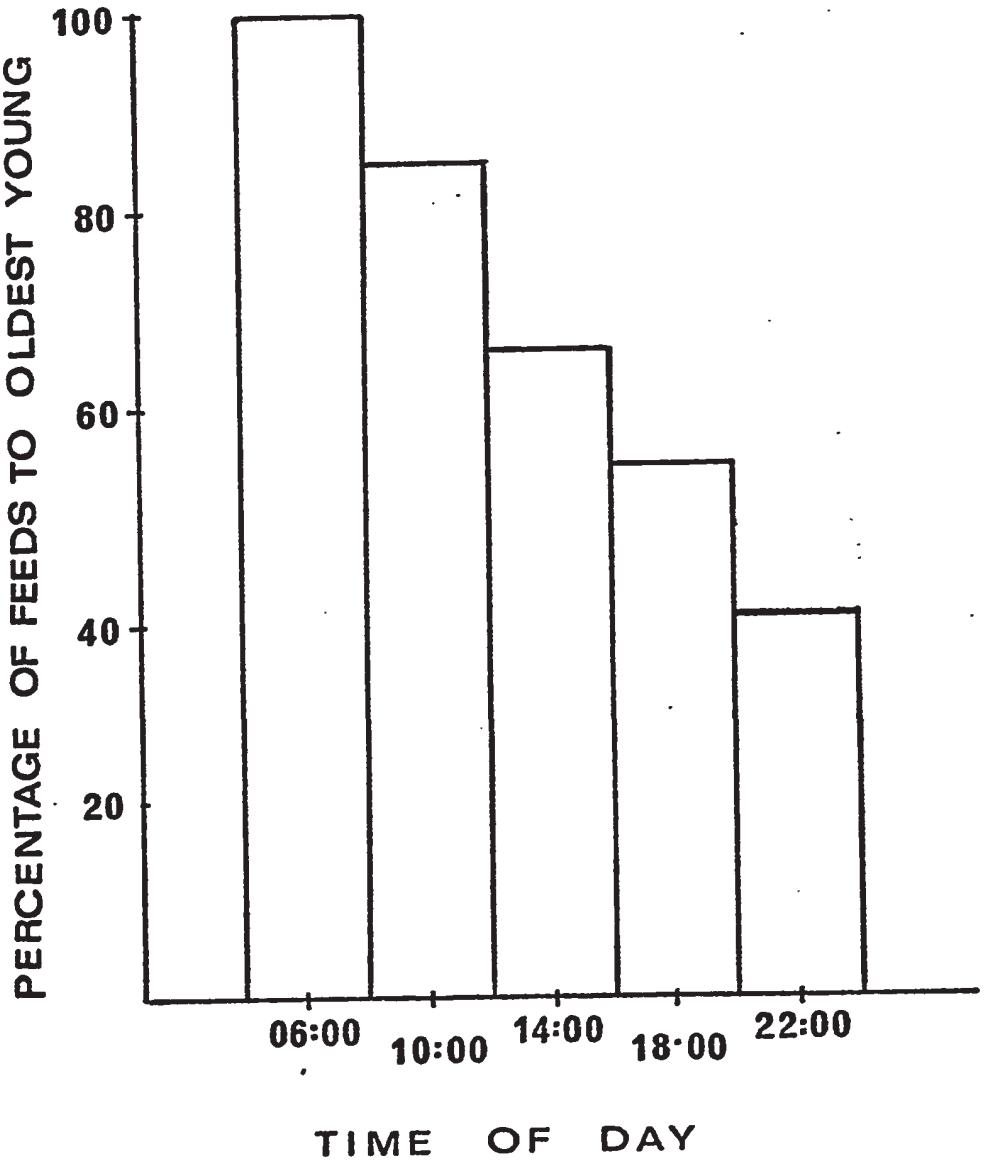

Figure 10. Percentage of feeds received by the older member of broods of two Red-throated Loons. Based on 94 feeds in 154 hours of observation at 3 nests at the McConnell River in 1969.

All 6 feeds before 08:00 were taken by the first hatched chick. The period 08:00 to 16:00 was compared with the period 16:00 to 24:00 for equal feeding by each young (table 46). The first hatched received a significantly higher proportion of food in the middle than in the last period ($\chi^2 = 6.826$; df = 1; $P<0.01$).

IV.2.D. Effect of Brood-size on Growth Rates

If the system of asynchronous hatching is adaptive then the older chick of broods of two should have an equal chance of survival as do chicks which are members of broods of one. The older chick should not be at a disadvantage because of the presence of its younger sib. It should survive and grow as well as chicks in broods of one.

Survival of marked broods is presented in table 47 which compares the success of first hatched chicks with broods which contain only one young. There was no difference in success between the two groups ($\chi^2 = 0.199$; df = 1; P = ns). The presence of the second young in broods of two does not adversely affect the survival rate of the first hatched young. Does it depress the growth rate of the first hatched?

The growth rates of first hatched young were calculated for those broods in which both young were still alive. Growth rates were also calculated for broods of one and the older chick in broods of two in which the younger chick died before it reached four days of age. Comparison of these two groups should

TABLE 46

NUMBER OF FISH EATEN BY FIRST HATCHED AND SECOND HATCHED CHICK PER DAILY TIME PERIOD (RED-THROATED LOON - 1969)

Time Period	First Hatched	Second Hatched	Total
0800-1600	35	10	45
1600-2400	22	21	43
Total	57	31	88

TABLE 47

SURVIVAL OF FIRST HATCHED CHICKS VERSUS SURVIVAL IN BROODS OF ONE (RED-THROATED LOON, 1968-69)

Class	Survive	Not Survive	Total
First hatched in broods of two	15	9	24
Broods of one	6	5	11
Total	21	14	35

reveal whether the presence of the living second young in broods of two depressed the growth rate of the older chick.

The regressions of size on age were calculated and are presented in table 48. The data for growth in weight were transformed to a log-log scale to facilitate comparisons of linear regressions.

None of the differences between groups of young for each growth measurement were significant. There was no difference in growth rates between first hatched young regardless of whether the second hatched young was still alive. This suggests that the second young only receives food after the first young has finished eating.

IV.2.E. Dominance within Broods

The first hatched member of a brood received more food than its younger sib (section IV.2.C). The behavioural aspects of this precedence by the older chick are analyzed in this section. The first hatched chick is a day older than its broodmate and is somewhat larger as a result. Does the older chick get more food merely because it is stronger than the younger one or is there a behavioural dominance between the brood members? A true dominance hierarchy requires that non-dominant animals behave as subordinates (Tinbergen 1953a:71; Allee 1958; Armstrong 1965:255). Thus a dominance hierarchy is more than one animal defeating another whenever they meet by chance. It is a stable system in which violence is

TABLE 48

COMPARISON OF GROWTH OF YOUNG IN BROODS OF ONE WITH GROWTH OF OLDER YOUNG IN BROODS OF TWO (WHEN BOTH SIBS ALIVE) - RED-THROATED LOONS, 1969

	Class	Regression Coefficient	F-value for H_o: $\beta = 0$	DF	t-value for H_o: $\beta_1 = \beta_2$	DF
Tarsus	Single[1]	1.658	1399.53***	1,56	-1.388^{ns}	91
	Older[2]	1.781	702.30***	1,35		
Culmen	Single	0.853	1987.36***	1,56	-0.934^{ns}	91
	Older	0.888	1028.42***	1,35		
Weight[3]	Single	0.783	738.21***	1,56	0.540^{ns}	99
	Older	0.756	327.09***	1,43		

*** P 0.001

1. Single young in broods of one.
2. Older of 2 young in broods of 2 when both alive.
3. Weight data transformed to a log-log scale.

minimized, primarily by avoidance behaviour of subordinate animals. The hierarchy requires active behaviour by all members of the group, not just the dominant ones. Several forms of avoidance behaviour were observed in second hatched Red-throated Loons.

During the first 2 weeks of life young loons were fed by one parent which foraged away from the nest pond while the other stayed on the nest pond with the brood. The young spent most of their time on shore with an adult. Thus, when the fishing adult landed on the nest pond with a fish, the young on shore were usually some distance from it. In marked broods it was possible to determine which chick made the first move towards the fish-carrying adult. The first chick which left the brooding adult or if they were on water, the first chick which swam toward the fish-carrying adult was called the 'first chick out'. The fish was eaten by a chick within 1 or 2 minutes of the adult's landing.

The 'first chick out' did not always get the fish. The data (table 49) are based on 132 hours of observation at 2 Red-throated Loon nests (Broods 1 to 14 days old). Seventy-eight of these hours were before 16:00 and 54 were after 16:00. When the older chick was 'first out' for the food it got it, but this was not always true for the younger chick which on 8 occasions when it was 'first out', failed to get the fish. These ratios are different ($P = 0.0007$ by Fisher's Exact Test). There were also 6 cases in which both young left the

TABLE 49

RELATIONSHIP OF YOUNG FED TO YOUNG WHICH FIRST ATTEMPTED TO GET THE FOOD (RED-THROATED LOON - 1969)[1]

Outcome	Young which first tried for food		
Young making first attempt	First hatched	Second hatched	Totals
Ate the fish	39	22	61
Did not eat the fish	0	8	8
Totals	39	30	69

1. Excluding 5 cases where neither young ate the fish.

brooding adult simultaneously. The older chick got the fish in all of these instances. Thus the older chick always got the fish when it was 'first out' and when the 2 chicks left at the same time.

When the brood is being fed, the actions of the chick which does not get the fish yields information about the motivational state of that bird. A chick may either contest the food or it may make no attempt to get it. When both chicks try for the food, a race develops with each chick running across the water towards the fish-carrying adult. There were 74 feedings in which all the activities of the young could be seen and only 23 of these involved races. This is a small proportion of feedings in which both chicks tried for the food during a period when one chick (second-hatched) was slowly starving.

The older chick won 19 races and the younger only 4 indicating that the older chick won more races than its younger sibling ($\chi^2 = 8.52$; df = 1; $P<0.005$ with χ^2 adjusted for continuity for the H_o; 19:4 = 1:1). In 3 of the 4 races won by the younger chick it was very close to the landing site of the incoming adult and the older chick was much further away. The younger chick had eaten the fish before the older one reached the feeding site.

In the 19 races won by the older chick; it started first in 7, second in 6, and both chicks started together in 6. The time of start did not bias the number of races won

by the older chick. In only 3 of the 19 races won by the first-hatched was there a fight for the fish. The younger chick started first in two of these and they started together in the third. In the other 16 cases the younger chick gave up and became passive when it was clear that the older chick was pursuing the food.

There were 23 races and 51 non-contests in the 74 documented feedings. A non-contest occurred when the non-feeding chick made no effort to get the fish. It either stayed on shore with the brooding adult or it entered the water and slowly approached the feeding adult reaching it after the other young had eaten the fish.

The non-contests were divided into those occurring before and after 16:00 and were classified according to which young was passive (table 50). It is evident that the older chick was more likely to be passive later in the day whereas the younger chick was passive earlier in the day ($\chi^2 = 7.46$; df = 1; $P<0.01$). These data agree with those on food intake throughout the day (section IV.2). The older chick became passive later in the day after it had eaten several fish but the younger chick was passive early in the day when it was presumably hungry after going 8 to 10 hours at night when no fish were brought to the pond. Most of these observations were made on nest R2-69 where the older chick weighed 54 g at hatch and the younger was 50 g. When the first hatched was 13 days old (the end of nest observations) it weighed 513 g

TABLE 50

NUMBER OF FEEDS, PER TIME PERIOD, IN WHICH A CHICK WAS PASSIVE (RED-THROATED LOON - 1969)

Number of feeds during which	Number of feeds		Totals
	before 16:00	after 16:00	
Older chick remains passive	6	12	18
Younger chick remains passive	24	9	33
Totals	30	21	51

and its sib was 352 g. At 30 days the first hatched weighed 1158 g and the second hatched weighed only 503 g. It is obvious that the second hatched chick was not getting enough food. However, it still remained passive early in the day when it was very hungry. This subservient pattern was in response to the dominance of the older chick.

The two loon broods were watched for 132 hours and all encounters between the young were noted. These represent minimal figures as young were occasionally out of sight when being brooded. These missed encounters are believed few in number as no aggression was noted on warm days when the young sat beside the sitting adult in open view.

An encounter was considered aggressive if one chick pecked at the other. These pecks were usually aimed at the head and neck area of the victim. The attacks ranged in intensity from 2 to 12 pecks, although each bout is considered equal in the following analysis.

The number of aggressive encounters was only 14 which was surprisingly few for such a long period of observation (1 attack per 9.4 hours). Thus if these encounters served to establish a dominance hierarchy, the system is very efficient with little excess violence. Sjolander (1968) found young Arctic Loons (hatched in an incubator) to be very aggressive towards each other. This was not the case with undisturbed Arctic or Red-throated Loon broods at the McConnell River. However when an observer caught the young

they violently attacked anything which moved, including the observer and their broodmate.

The winner of an encounter was the chick which pecked the other the most. In the majority of cases only one chick pecked the other. Ten of the 14 observed fights were won by the older chick. Two were classed as ties and the outcome of the other two was not seen. Thus without exception the first hatched won or tied all fights with the second hatched. No aggressive display postures were observed in the small young and it is likely that the observed fights represent the only means used by the older chick to establish dominance. The younger chick avoided situations in which it would have to compete with the older chick such as when the older chick was feeding.

Eleven fights were associated with feeding and three occurred when the brood was swimming quietly. In these three encounters the older chick attacked the younger chick and all occurred in the first 3 days after hatch. Six of the eleven fights associated with feeding occurred just after one young had eaten, 4 occurred just prior to feeding (all 4 won by the first hatched), and 1 fight happened when both young tried to eat a fish which was too big to swallow. Thus in 74 feedings only 4 actually involved a fight prior to a young loon eating the fish.

Ten of the 14 fights occurred from 0 to 3 days of age while only 4 occurred from 4 to 14 days (66 hours observation

during each period). The concentration of aggressive encounters may indicate that the hierarchy is established early and needs little re-enforcement.

It is obvious that a dominance hierarchy does exist and that it serves to reduce within-brood strife over a limited resource (food).

IV.2.F. Comparative Data for Arctic Loons

The data on growth and feeding rates of Arctic Loon chicks are incomplete. The growth rates appeared similar to those of Red-throated Loons but they were not analyzed statistically because of the small sample size. However, the data on feeding rates of young Arctic Loons were extensive enough to permit analysis.

Young Arctic Loons at the McConnell River were fed exclusively by the parents. The majority of this food was gathered on the nesting territory with only an occasional fish brought in from Hudson Bay where the adults feed themselves. On the main study area the young were fed primarily on invertebrates and with a few pond fish when available.

The invertebrate prey were small and of approximately constant size. The invertebrates were visible in the adult's bill and they were fed to the young, one at a time. The following analysis assumes that each item is similar and that there is no bias in food size with respect to which young is fed.

Three marked broods were observed for varying lengths

of time. The data from an all day watch are presented in table 51 for a brood of two aged 4 and 3 days. All the fish were small freshwater species of about 5 cm based on comparison with an average adult bill length of 5.39 cm (mean of 3 males and 2 females from the McConnell River).

The two young had almost exactly the same number of feeds over the course of the day. This differed from the Red-throated Loons where the first hatched chick received significantly more food than the second hatched.

When the data are partitioned by time of day, the first hatched young received significantly more invertebrates before 16:30 and the second hatched received more after 16:30 ($\chi^2 = 7.663$; df = 1; $P<0.01$ for the H_o; 101:74 = 98:126). The intake of fish followed the same pattern with the first hatched getting the early fish. These data indicate that when the older young had received enough food the second young began to get a higher proportion of the food. This pattern also occurred in Red-throated Loons but there was not enough food and the second young was unable to equal the food intake of the first hatched. In this particular Arctic Loon brood both young were alive at four weeks of age when the study was terminated.

The above Arctic Loon brood was also observed on two other days (ages 3, 2 and 7, 6 days) for 6.5 hours, before 16:30 on each day. The first hatched chick received 152 invertebrates and the second hatched received 104. No fish

TABLE 51

FEEDING RATES OF YOUNG ARCTIC LOONS (1969)

Time	Type of Food	Number of feeds to First hatched	Number of feeds to Second hatched	Totals
06:25 -16:30	Invertebrate	101	74	175
	Fish	2	0	2*
16:30 -22:30	Invertebrate	98	126	224
	Fish	0	3	3
Totals	Invertebrate	199	200	399
	Fish	2	3	5

*Does not include 3 fish fed during this period but not known to which young.

were fed in these periods. These data confirm the theory that first hatched young receive more food before 16:30 hours ($\chi^2 = 9.00$; df = 1; $P<0.005$ for the H_o; 152:104 = 1:1).

This Arctic Loon territory was also observed briefly in 1968 when the brood was 7 and 6 days old respectively. These observations were made after 16:30 and they revealed a different feeding pattern than in 1969 (table 52). The second hatched young received less food in 1968 ($\chi^2 = 4.199$; df = 1; $P<0.05$) than in 1969. This was during the time of day when the second hatched should have been getting more food and catching up to the first hatched chick. Correlated with these feeding differences was the fact that the second hatched young survived in 1969 but disappeared in 1968, three to six days after the feeding data were collected.

One other nest was observed in 1969 from 15:30 to 20:30 when the young were 2 and 1 days old. At this time of day the second hatched should have been receiving a high proportion of the food. In fact the first hatched ate far more (86 invertebrates) than its sib (34 invertebrates). These differences are highly significant ($\chi^2 = 21.675$; df = 1; $P<0.005$ with χ^2 adjusted for continuity). It is not surprising that the second hatched young disappeared within a week.

Although the data for Arctic Loons are fragmentary they support the findings for Red-throated Loons. That is, the first hatched young receives food first and the second

TABLE 52

NUMBER AND RATIO OF FEEDS TO ARCTIC LOON BROODS IN TWO YEARS[1]

Year	Number of invertebrates fed to		Totals
	First hatched	Second hatched	
1968	111	96	207
1969	98	126	224
Totals	209	222	431

1. Only observations after 16:30 hours are included.

hatched gets a substantial amount only after the older chick is satisfied. If enough food is available then the second young also survives.

IV.3. ANNUAL DIFFERENCES IN GROWTH RATE AND SURVIVAL

Growth rates for Red-throated Loons were compared for 1968 and 1969. Only broods of one and the oldest member of broods of two were used in each year.

The linear regression of size on age was significant for each measurement for both years (table 53). The comparison between years reveals that Red-throated Loons in 1969 grew significantly faster than in 1968. This applies to all three measurements.

These differences between years were correlated with the amount of food brought to the young. It was not possible to directly compare feeding rates between years because of the amount of time such a comparison would have required. However, an index of food availability was provided by the feeding behaviour of the adult Red-throated Loons. The adults bring food from Hudson Bay to their young. The main flight-lane to the coast was down the McConnell River. Conversely when the adults returned with food, they flew up the river and then turned south to their nest ponds. By watching the adults returning from the sea it was possible to calculate the proportion which were carrying fish for their young. All food brought to the young was fish and these were carried cross-

TABLE 53

COMPARISON OF GROWTH RATES OF RED-THROATED LOONS IN 1968 and 1969[1]

	Year	Regression coefficient[2]	F- value for H_o $\beta = 0$	df	t-value for H_o $\beta_1 = \beta_2$	df
Tarsus	1968	1.457	171.76***	1,25	2.51*	118
	1969	1.690	2199.78***	1,93		
Culmen	1968	0.736	216.46***	1,25	3.12**	118
	1969	0.861	3207.77***	1,93		
Weight[3]	1968	0.644	259.88***	1,45	3.19**	146
	1969	0.781	1030.40***	1,101		

* P<0.02, ** P<0.01, *** P<0.001

1. Based on broods of one and older member of broods of two.
2. Measurement regressed on age.
3. Weight data transformed to a log-log scale.

wise in the adult's bill and were clearly visible. Adults were watched, as other work permitted, between 12:00 and 21:00 hours over an 18 day period in 1968 (23 hours of observation) and a 25 day period in 1969 (15 hours of observation). During these periods the majority of nests had hatched and single adult Red-throated Loons which returned from the coast without fish were considered to have been unsuccessful in their attempt to feed their young. Loon broods were fed regularly throughout the day and food availability was apparently unaffected by tide levels on Hudson Bay.

There was a striking difference in the proportion of adults which were carrying fish (table 54) in the 2 years. In 1969 virtually all Red-throated Loons carried fish whereas in 1968 about half had fish. These differences are highly significant ($\chi^2 = 25.233$; $df = 1$; $P<0.005$) and indicate that fish were more available to adults in 1969. The reasons for this difference in food availability are unknown. Red-throated Loons were not observed feeding anything but fish to their young.

The survival rates of Red-throated Loon chicks are presented in table 55 and reveal that most of the 1968 mortality occurred in the first 10 days. This high early mortality was expected in view of the lower feeding rates in 1968.

In the longer run of 30 days the survival rates were the same for 1968 and 1969. However, it should be remembered that chicks in 1969 were larger and presumably in better

TABLE 54

NUMBER OF ADULT RED-THROATED LOONS CARRYING FISH UPRIVER

	With fish	Without fish	Total
1968	41	40	81
1969	45	3	48
Total	86	43	129

TABLE 55

SURVIVAL OF RED-THROATED LOON CHICKS

Year	Number Hatched	Percent of young alive on			Number alive at day 30
		Day 10	Day 20	Day 30	
1967	21	76.2	57.1	47.6	10
1968	33	45.5	39.3	39.3	13
1969	45	76.5	48.9	37.8	17

condition than those in 1968.

It seems that food availability was different from year to year and these differences were reflected in growth and survival patterns.

V. CLUTCH SIZE IN ARCTIC AND RED-THROATED LOONS

In view of the low survival rate of the second young in a two young brood, why do loons lay two eggs? The obvious answer is that in good feeding periods and areas the adults are able to raise the second young and this occurs frequently enough to maintain the two egg clutch in the population. Two egg clutches may also have other attributes which give them greater survival potential than one egg clutches. These attributes are analyzed in the following sections.

V.A. Number of Eggs

Clutch size was determined for 178 loon nests (table 56). No cases of more than two eggs in a nest were found. Some of the nests with one egg clutches may have lost a second egg before I first visited them. This accounts for an unknown proportion of the one egg clutches. It does not account for them all as loons of both species did lay single egg clutches. This was verified in five nests watched continuously from an observation tower during the laying period (3 Arctic and 2 Red-throated Loon nests).

Clutch size was the same in each of the three years for a particular species ($\chi^2 = 4.433$; df = 2; P is NS for Arctic Loons and $\chi^2 = 0.448$; df = 2, P is NS for Red-throated Loons (table 56).

Comparing the species totals in table 56 reveals that

TABLE 56

CLUTCH SIZE IN ARCTIC AND RED-THROATED LOONS - 1967 to 1969[1]

Species	Year	Number of clutches with		Totals	Mean clutch size
		two eggs	one egg		
Arctic Loon	1967	23	12	35	1.65
	1968	17	8	25	1.68
	1969	27	4	31	1.87
	Totals	67	24	91	1.74
Red-throated Loon	1967	24	6	30	1.80
	1968	20	3	23	1.87
	1969	28	6	34	1.82
	Totals	72	15	87	1.83

1. Re-nesting attempts excluded.

there was no difference in clutch size between the two species ($\chi^2 = 2.168$; df = 1; P is NS).

There was a substantial number of one-egg clutches every year; possibly certain birds were prone to lay only one egg while others usually laid two. This was analyzed in the following manner based on the assumption that the same pair occupied the same territory in successive years. This assumption is supported by circumstantial evidence (section I.1.A).

The proportion of two-egg clutches was calculated for each species for each year from the data in table 56 (e.g. in 1967, 24 of 30 Red-throated Loon nests had 2 eggs for a probability of 0.8000 that a Red-throated Loon nest will have 2 eggs in 1967). The corresponding figures for 1968 and 1969 were 0.869565 and 0.823529 respectively. Now consider a pair whose clutch was known for each of the three years. The probability of it having a two-egg clutch in all three years was 0.8000 X 0.869565 X 0.823529 = 0.572890.

It is possible to determine the expected probability for each combination of clutch sizes over the three year period. Multiplying these probabilities by the number of pairs with known clutch sizes in the three years gives the expected number of pairs with each combination of clutch sizes. These expected values can be compared with the observed values and a chi-square analysis for differences can be performed.

The data are presented in tables 57 and 58. The chi-square values were calculated on pooled classes due to small sample size and low expected values. Three groups were recognized; nests with 3 two-egg clutches, nests with only one one-egg clutch, and those with 2 or 3 one-egg clutches.

The results of Arctic Loons indicate that one-egg clutches were concentrated on certain pairs ($\chi^2 = 8.745$; df = 2; $P<0.025$). The same trend occurred in Red-throated Loons but was not significant ($\chi^2 = 4.111$; df = 2; $0.2>P>0.1$). There were more birds laying one egg in more than one year than was expected on the basis of chance alone.

Pairs in which the clutch was known for only two years support these findings. An overall probability for two-egg clutches can be calculated since the clutch size was the same in each year (section V.1). Thus the probability of a clutch having two eggs was 0.736264 for Arctic Loons and 0.827586 for Red-throated Loons based on the total three year data.

There were 11 Red-throated Loon nests with 2 known clutches and 10 of these had two eggs in both years compared to an expected value of 7.53. Seven of eleven Arctic Loon nests with 2 clutches had two eggs in both years compared to an expected value of 5.91 nests. These samples are too small to test but they suggest that more pairs laid two-eggs in both years than was indicated by chance alone.

There was a trend towards pairs having the same clutch size from year to year. It is not known whether these were

TABLE 57

CONSTANCY OF CLUTCH SIZE WITHIN PAIRS OF ARCTIC LOONS[1]

Clutch size in 1967-68-69	Expected Probability[2]	Expected Number of Pairs	Observed Number of Pairs	Pooled Values	
				Expected	Observed
2 - 2 - 2	0.389	8.56	10	8.56	10
2 - 2 - 1	0.057	1.27	1		
2 - 1 - 2	0.183	4.03	0	9.77	4
1 - 2 - 2	0.203	4.47	3		
2 - 1 - 1	0.027	0.60	2		
1 - 2 - 1	0.030	0.66	1		
1 - 1 - 2	0.095	2.10	4	3.67	8
1 - 1 - 1	0.014	0.31	1		
Totals	0.998	22.00	22	22.00	22

1. See text for methodology

2. Probability of having a 2-egg clutch was 0.657143 in 1967; 0.680000 in 1968; 0.870968 in 1969.

TABLE 58

CONSTANCY OF CLUTCH SIZE WITHIN PAIRS OF RED-THROATED LOONS[1]

Clutch size in 1967-68-69	Expected Probability[2]	Expected Number of Pairs	Observed Number of Pairs	Pooled Values	
				Expected	Observed
2 - 2 - 2	0.573	8.59	9	8.59	9
2 - 2 - 1	0.123	1.84	1		
2 - 1 - 2	0.086	1.29	0	5.28	3
1 - 2 - 2	0.143	2.15	2		
2 - 1 - 1	0.018	0.28	1		
1 - 2 - 1	0.031	0.46	0	1.13	3
1 - 1 - 2	0.021	0.32	1		
1 - 1 - 1	0.004	0.07	1		
Totals	0.999	15.00	15	15.00	15

1. See text for methodology.

genetic differences or behavioural differences which affected the loss of one egg almost as soon as it was laid.

V.B. Size of Eggs

In 1969 I weighed loon eggs during routine nest visits. The length and width were measured to the nearest 0.1 mm with dial calipers and the weight was taken to the nearest gram.

The weight of the egg decreases as incubation progresses and this makes it difficult to use weight in comparisons unless the original weight at laying is known. This was rarely the case as I did not want to disturb the birds during the laying period. Thus weight was not used in this analysis. However, it was possible to pool the weight measurements and calculate a linear regression of weight decrease with age in days. This relationship is described by the equation $Y = 101.068 - 0.5508X$ for Arctic Loons and $Y = 85.946 - 0.6628X$ for Red-throated Loons. The regression coefficients are highly significant ($F = 9.918$; $df = 1,55$; $P<0.005$ for Arctic Loons and $F = 31.453$; $df = 1,89$; $P<.001$ for Red-throated Loons). These equations yield calculated initial egg weights of 101 g for Arctic Loons and 86 g for Red-throated Loons.

It is shown in section IV that the first egg of a two-egg clutch had a much higher probability of producing a successful young than did the second egg. This was attributed to parental feeding behaviour and a within-brood dominance hierarchy. However these differences in chick survival might

have resulted from differences in female quality (Zwickel and Bendell 1967), in egg quality (Watson and Moss 1971) or egg quantity (of energy reserves) within the clutch. To test this hypothesis the first and second eggs of two-egg clutches were compared for external differences.

If some loons have trouble obtaining enough energy for a full clutch of eggs then the second egg should be more variable in size than the first egg. This was not the case in either species as the first and second eggs were equally variable for length and for width (Red-throated Loon: $F = 1.487$ for egg length and $F = 1.089$ for egg width with $df = 13,13$ and P is NS. Arctic Loon: $F = 1.505$ for length and $F = 1.728$ for width with $df = 10,10$ and P is NS).

There were no differences in size between the first and second eggs of the same clutch (table 59). This held for length and width in both species. It was also true for 'elongation' which is a simple measure of egg shape derived by dividing the length of an egg by its width. Egg size was not a factor affecting the subsequent differential survival of chicks in the same brood.

There were a few clutches of only one egg and it was possible that these eggs were different from those in two-egg clutches. Egg size differences might have been correlated with the clutch-size differences. In fact, there were no differences in the egg-sizes or shapes for the two clutch sizes (table 60). This was true for both species.

TABLE 59

COMPARISON OF THE SIZE OF EGGS IN TWO-EGG CLUTCHES (1969)[1]

		First egg	Second egg	t^2	df
Red-throated Loon	Mean length (mm)	72.47	72.89	-0.664^{ns}	13
	Mean width (mm)	45.67	45.29	1.146^{ns}	13
	Elongation	1.587	1.610	-1.341^{ns}	13
Arctic Loon	Mean length (mm)	76.85	76.19	0.634^{ns}	10
	Mean width (mm)	48.59	47.91	1.965^{ns}	10
	Elongation	1.583	1.591	-0.269^{ns}	10

1. Based on 14 Red-throated Loon and 11 Arctic Loon clutches.

2. t value for paired observations.

TABLE 60

COMPARISON OF EGG-SIZE IN ONE AND TWO-EGG CLUTCHES (1969)

		Two-egg clutch		One-egg clutch		t^1
		Mean	N	Mean	N	
Red-throated Loon	Length (mm)	72.68	28	72.83	5	0.095^{ns}
	Width (mm)	45.48	28	45.66	5	0.281^{ns}
	Elongation	1.599	28	1.595	5	-0.089^{ns}
Arctic Loon	Length (mm)	76.52	22	79.73	3	1.468^{ns}
	Width (mm)	48.25	22	48.50	3	0.249^{ns}
	Elongation	1.587	22	1.644	3	1.125^{ns}

1. t test with df = 31 for Red-throated Loons and df = 23 for Arctic Loons.

It has been shown that there were no differences between the eggs within a two-egg clutch or between one and two-egg clutches. It was apparent, however, that there were differences between different two-egg clutches. The hypothesis that clutches were the same size, was tested by Analysis of Variance and was rejected for both species (Red-throated Loon: F for length = 7.549, $P<.001$; F for width = 3.466, $P<0.025$; F for elongation = 2.034, P is NS with df = 1,13. Arctic Loon: F for length = 3.629, $P<0.05$; F for width = 7.431, $P<0.005$; F for elongation = 2.012, P is NS with df = 1,10). There were significant inter-clutch size differences. This raises the possibility that the differences in success among young of different females were related to egg-size.

A large egg may have greater energy reserves and produce a more vigorous chick which presumably would have greater survival potential than a chick from a smaller egg. This was tested for loons by comparing chick survival with the size of the egg which produced the chick. I assumed that the larger energy reserves of larger eggs would be most important to the chick in the period immediately following hatching. At two weeks of age the health of the chick would be independent of egg reserves and differential survival beyond this age would also be independent of these reserves. However, survival during the first two weeks could be directly affected by these energy reserves. Chicks were classed as those which died before two weeks of age and those that survived longer

than two weeks. If initial egg size was important, it would be expected that chicks surviving over 14 days would come from larger eggs than chicks not surviving this long. This was tested in table 61 where only the first egg of two-egg clutches were considered. There were no differences in success of young in relation to egg-size in Red-throated Loons. It was not possible to test Arctic Loons as not enough broods were marked.

There is no evidence to suggest that egg-size has any effect on the production of young loons.

V.C. Survival of Eggs

Do the eggs in a two-egg clutch survive longer than those in one-egg clutches? If the two clutch sizes have differing survival potentials then it may explain the retention of the two sizes in the system.

This analysis was based on the survival of eggs to the expected time of hatch. An infertile egg was considered successful if it survived for the full incubation period. Thus, this section analyzes parental care and protection of the eggs from predators.

It is possible that a two-egg clutch was more visible to predators than was a one-egg clutch and this would bias the egg-loss results against two-egg clutches. It was unlikely that the reverse situation occurred where one-egg clutches were more visible.

The first point to examine is whether two-egg and one-

TABLE 61

RELATIONSHIP BETWEEN EGG-SIZE AND CHICK SURVIVAL IN RED-THROATED LOONS (1969)

	Size of eggs from which young survive				t^1
	14 or fewer days		over 14 days		
	Mean	N	Mean	N	
Length (mm)	71.10	4	73.02	10	1.063^{ns}
Width (mm)	45.06	4	45.91	10	1.077^{ns}

1. t test with df = 12.

egg clutches survive equally well. Table 62 compares the number of nests with one and two eggs and the number of each losing at least one egg, for each species in three breeding seasons. The proportion of Red-throated Loon nests losing at least one egg was not significantly different for one and two-egg clutches ($\chi^2 = 2.42$; df = 1; P is NS for H_o, 21:40 = 7:5). The data for Arctic Loons yielded a similar result ($\chi^2 = 3.76$; df = 1; $0.05<P<0.1$ for H_o, 18:40 = 12:10). This is very close to the 0.05 significance level of $\chi^2 = 3.84$. The results for both species indicated a trend towards two-egg clutches being less likely to lose an egg than were one-egg clutches but the small sample size masks statistically significant differences. I therefore pooled the data for both species.

Pooling the data was a valid procedure for two reasons. The two species are congeneric and it is likely that the clutch-size of loons is a genetic character as all loon species have a clutch of one or two eggs with two being the usual number (Palmer, 1962). The two species also had the same distribution of values in table 62 ($\chi^2 = 2.80$; df = 3; P is NS for H_o, 21:40:7:5 = 18:40:12:10). Therefore there was biological and statistical validity for pooling the two species in a 2 X 2 contingency table (table 63). The results indicated that there was indeed a greater probability of one-egg clutches losing an egg than of two-egg clutches ($\chi^2 = 5.99$; df = 1; $P<0.025$).

TABLE 62

MORTALITY OF EGGS IN ARCTIC AND RED-THROATED LOON NESTS

GROUPED BY INITIAL CLUTCH SIZE

Species	Year	Two-egg clutches			One-egg clutches		
		Number of nests	Number of nests losing at least one egg	Number of nests with no egg loss	Number of nests	Number of nests losing at least one egg	Number of nests with no egg loss
Red-throated Loon	1967	18	6	12	5	4	1
	1968	17	8	9	3	1	2
	1969	26	7	19	4	2	2
	Totals	61	21	40	12	7	5
Arctic Loon	1967	17	7	10	11	6	5
	1968	18	6	12	8	6	2
	1969	23	5	18	3	0	3
	Totals	58	18	40	22	12	10

TABLE 63

MORTALITY OF EGGS IN ONE AND TWO-EGG CLUTCHES

WITH DATA POOLED FOR ARCTIC AND RED-THROATED LOONS

Clutch size	Number of nests losing		Totals
	at least one egg	no eggs	
2	39	80	119
1	19	15	34
Totals	58	95	153

Another way of approaching the problem was to examine the number of clutches losing all their eggs. Ten of 50 Arctic Loon nests with two eggs lost them both and 12 of 22 one-egg clutches were lost. These loss-rates were significantly different ($\chi^2 = 8.59$; df = 1; $P<0.005$). Fifteen of 55 two-egg clutches of Red-throated Loons were lost whereas 7 of 12 one-egg clutches were destroyed. These rates were also different ($\chi^2 = 4.95$; df = 1; $P<0.05$). In both species of loons two-egg clutches were less likely to be completely lost than were one-egg clutches.

What was the fate of two-egg clutches which lost one egg? Does the remaining egg have the same chance of hatching as an egg in a single egg clutch? There were 14 cases where a nest lost one egg of a two-egg clutch. In all cases (8 Arctic Loons and 6 Red-throated Loons) the remaining egg survived until hatching time. Comparisons of the success rate of this second egg with the eggs from one-egg clutches yields a P = 0.007 for Arctic Loons (H_o, 8:0 = 10:12) and a P = 0.0249 for Red-throated Loons (H_o, 6:0 = 5:7) by Fisher's Exact Test. Thus, on a per nest basis, one-egg clutches have a lower success rate than the remaining egg in a two-egg clutch which lost one egg.

The increased success of the remaining egg could have been due to improved parental care by parents which learned from the loss of one egg. This could not happen in one-egg clutches. Alternatively, predation could have been random and

the higher success of the remaining egg of a two-egg clutch could have been due to the lowered probability of the same nest suffering random predation twice during incubation. This was tested by comparing the loss per day of egg exposure by both groups (table 64). If predation was random then the remaining egg from two-egg clutches and the egg from one-egg clutches should have the same loss rate per day.

The numbers of egg days in table 64 were derived in the following manner. The totals for the remaining egg of two-egg clutches were based on the number of days the eggs could have been lost after the first egg was taken by predators. The number of days for surviving one-egg clutches was based on average incubation periods of 26 days for Arctic Loons and 25 days for Red-throated Loons. It was not possible to determine accurately the stage of incubation at which single egg clutches disappeared since I aged most eggs by back-dating from the time of hatch rather than trying to find nests during laying. I used the average time of loss of the first egg of two-egg clutches to estimate the length of time one-egg clutches were subject to predation before they were actually lost (14 days for Arctic Loons and 9 days for Red-throated Loons).

There was no difference in the rate of egg-loss per day for one-egg clutches and the remaining eggs of two-egg clutches for Red-throated Loons ($\chi^2 = 2.15$; df = 1; P is NS). The

TABLE 64

EGG-LOSS PER EXPOSURE DAY IN ARCTIC AND RED-THROATED LOONS

Species	Clutch size	Number of egg days with		Totals
		no egg loss	egg loss	
Arctic Loon	Remaining egg of two-egg clutch	138	0	138
	One-egg clutch	368	12	380
	Totals	506	12	518
Red-throated Loon	Remaining egg of two-egg clutch	67	0	67
	One-egg clutch	216	7	223
	Totals	283	7	290

differences were significant for Arctic Loons ($\chi^2 = 4.46$; df = 1; $P<0.05$). The trends for the two species were similar and the combined values yield significant differences ($\chi^2 = 6.61$; df = 1; $P<0.025$).

It is evident that the remaining eggs in two-egg clutches had a lower loss-rate per exposure day than did single egg clutches. The difference was more pronounced in Arctic Loons which was a function of a greater number of exposure days for remaining eggs of two-egg clutches in this species. The loss-rate per exposure day for one-egg clutches was the same for both species ($\chi^2 = 0.00016$; df = 1; P is NS).

The difference in loss-rate per day for the two groups indicated that an external factor was over-riding chance predation. The obvious factor was learning by the adults which lost an egg and were then better able to protect the remaining egg. These adults were probably already quite attentive to the nest since they were able to save one of the two eggs. Many other pairs were inattentive to the point of losing both eggs at once.

There is a possibility that some nests with two eggs lost one egg and then the other in unrelated incidents between nest vists. These nests would then be classed as having lost both eggs at once. It is assumed that such cases were rare since in the 14 instances when a visit to a two-egg nest revealed that one egg had been lost, the remaining egg

was never lost. In 13 of the 25 cases (both species) the full clutch was lost between two visits which were five or fewer days apart. It was unlikely that two unrelated incidents of predation occurred at the same nest within this short period. Fully 5 of the remaining 12 cases could have been nests losing both eggs independently and it would still yield a significant interaction χ^2 of 4.30 (df = 1; $P<0.05$ for the H_o, 14:5 = 15:19) for the hypothesis of equal egg-loss between one-egg clutches and two-egg clutches which lost an egg. Therefore it seems safe to treat the 25 cases, where both eggs of a two-egg clutch disappeared between consecutive nest-visits, as actually involving nests which lost both eggs in one predation incident.

Another potential sampling artifact was the inclusion of nests losing one egg before the first visit in the category of one-egg clutches. This leads to the following results when comparing the success rates of one-egg clutches with the remaining egg in two-egg clutches. It will make no difference if the success rates of the two groups were the same. If one-egg clutches were more successful then inclusion of two-egg nests which lost an egg, in this group will mask any true differences in success. If the two to one-egg nests were more successful than true one-egg nests then their inclusion in the one-egg category will also mask any real differences. Thus if differences still show up then it means that they are real and few clutches have been mis-identified.

The main conclusions of this section therefore are

that: two-egg clutches were less likely to lose eggs than were one-egg clutches, and when they did lose one egg the remaining egg had a higher survival rate than a single egg clutch.

V.D. Causes of Egg Loss

The main cause of egg-loss was predation (one Red-Throated Loon nest was lost due to local flooding). The chief egg predators were Parasitic Jaeger, Herring Gull, Sandhill Crane (Grus canadensis) and Arctic Fox.

It was not always possible to determine what predator destroyed a loon nest. Foxes and cranes often left tracks near the nest. Gulls usually carried the egg away and left no trace whereas the Parasitic Jaeger usually punctured the eggs on the nest but occasionally carried the smaller Red-throated Loon eggs away.

Section V.C documents the number of eggs lost. The Parasitic Jaeger took more loon eggs than all other predators combined. They roamed the study area in loose flocks looking for unattended eggs. The Jaeger could land at a nest immediately on finding it unless the adult loon was within a few feet of it. The jaeger punctured the loon egg almost as soon as it landed at the nest. The whole process often took only a few seconds placing a premium on attentive behaviour in adult loons.

The predation rate on the study area was undoubtedly

higher than in other areas, for two reasons. First, the mere fact of human visitation must have some detrimental effect on reproductive success of any bird species but particularly so in flat, open tundra regions where flocks of avian predators follow an observer. Second, the huge Blue Goose (Chen caerulescens) colony at the McConnell River attracts large numbers of avian predators (Harvey 1971; this study) particularly non-breeding flocks of Parasitic Jaegers, Herring Gulls, Thayer's Gulls (Larus thayeri), and smaller numbers of Pomarine Jaegers (Stercorarius pomarinus). These predators, although attracted by the estimated 50,000 nests of Blue Geese, took many loon eggs especially when the goose eggs were near hatching and well protected by the geese.

V.E Production of Young

This section examines the probability of an egg producing a live young. It therefore includes infertile and addled eggs as unsuccessful even though they may have been protected until the normal time of hatch.

The first question is whether the production of young per egg was the same in all three years. Due to the small numbers of one-egg clutches in each year, these were grouped with two-egg clutches to give a pooled hatch:non-hatch ratio for each year. These data are presented in the right hand section of table 65. The not-hatch category includes all eggs which were predated, infertile, or somehow lost.

TABLE 65

NUMBER OF YOUNG PRODUCED PER EGG BY ARCTIC LOONS AND RED-THROATED LOONS

Year	Number of eggs in two-egg clutches which			Number of eggs in one-egg clutches which			Number of eggs in all clutches which		
	hatched	did not hatch	Total	hatched	did not hatch	Total	hatched	did not hatch	Total
Arctic Loon									
1967	22	12	34	5	6	11	27	18	45
1968	28	8	36	2	6	8	30	14	44
1969	34	12	46	3	0	3	37	12	49
Total	84	32	116	10	12	22	94	44	138
Red-throated Loon									
1967	22	14	36	0	5	5	22	19	41
1968	23	11	34	2	1	3	25	12	37
1969	42	10	52	2	2	4	44	12	56
Total	87	35	122	4	8	12	91	43	134

The loss rate of eggs was the same in all three years for the Arctic Loon ($\chi^2 = 2.59$; df = 2; P is NS). However, the loss rate was not the same in all three years for the Red-throated Loon ($\chi^2 = 6.74$; df = 2; $P<0.05$). Most of this latter difference was due to the high mortality in 1967 (56.7% of the χ^2).

It is probable that the higher mortality in 1967 was due to nest visitation by an inexperienced observer. Practice is required to judge whether an observer can visit a loon nest and then retreat to a safe distance before the ever present Parasitic Jaegers can find and destroy the nest. This problem was particularly severe for Red-throated Loons as they nested in small inconspicuous ponds and were often inadvertently flushed from their ponds in areas which were unfamiliar to the observer. Arctic Loons nested on larger ponds and rarely were accidentally flushed, even by an inexperienced observer.

Thus the gradual increase in the success of eggs with years probably reflects nothing more than the increased competence of the observer. The 1969 figures for both species may represent a true hatching rate with minimal human interference. It seems best to assume that there were no annual biological differences in the ability of eggs to produce live young.

The next question is whether the eggs in one and two-egg clutches have the same probability of producing a live

young. In Arctic Loons each egg in a two-egg clutch has a significantly greater chance of producing a live young than eggs in one-egg clutches ($\chi^2 = 6.19$; df = 1; $P<0.025$ for the H_o; 84:32 = 10:12 from table 65). A similar result was obtained for Red-throated Loons ($\chi^2 = 7.23$; df = 1; $P<0.01$ for the H_o; 87:35 = 4:8).

The hatching probability per egg laid in a two-egg Arctic Loon nest was 0.724 and it was 0.454 in one-egg clutches. The comparable figures for Red-throated Loons were 0.713 young per egg laid for two-egg clutches and 0.333 for one-egg clutches. The species showed no differences in these ratios ($\chi^2 = 3.50$; df = 3; P is NS for the H_o; 84:32:10:12 = 87:35:4:8).

In terms of production of young the two-egg clutch was more successful per egg than a one-egg clutch in both species. On a per nest basis the number of young hatched per nest in two-egg clutches was 1.45 as opposed to only 0.454 for one-egg clutches for Arctic Loons. The ratio of young hatching per nest for Red-throated Loons was 1.43 and 0.33 for two and one-egg clutches respectively. It was advantageous to lay clutches of two eggs even though the second young usually did not survive because an egg in a two-egg clutch was more likely to produce a young bird in the first place than was a one-egg clutch.

V.F. The Effect of Brood Size on Chick Success

What is the probability that young loons from broods of different sizes survive equally well? Does brood size affect survival rate of young loons? Young were considered to be raised successfully if they were alive at my last visit to the nest pond. The chick must have been at least two weeks of age and most were between three and five weeks old. The data appear in table 66.

Broods with an initial size of one young came from two sources; those two-egg clutches which lost one egg before hatch and true one-egg clutches. It was possible that these two groups could have had differential effects on chick survival. This was tested using the data from table 66. There was no difference in the success rate of the two classe in Arctic Loons ($\chi^2 = 0.259$; df = 1; P is NS for the H_o; 8:3 = 9:2) or for Red-throated Loons ($\chi^2 = 0.152$; df = 1; P is NS for the H_o; 6:4 = 3:3). There was no difference in the young produced from clutches of one-egg and two-egg clutches which lost an egg.

It is now possible to test the success rate for broods of one compared with broods of two (table 66). There was no difference in the number of broods of each size which raised at least one young. This was true for both Arctic Loons ($\chi^2 = 2.97$; df = 1; P is NS for the H_o; 29:2 = 17:5) and Red-throated Loons ($\chi^2 = 0.155$; df = 1; P is NS for the H_o; 26:16 = 9:7).

TABLE 66

CHICK SUCCESS IN RELATION TO INITIAL BROOD SIZE IN ARCTIC AND RED-THROATED LOONS (1967-68-69)

Species	Initial Clutch Size	Initial Brood Size	Number of Broods	Number of pairs raising		
				2 young	1 young	0 young
Arctic Loon	2	2	31	8	21	2
	2*	1	11	-	8	3
	1	1	11	-	9	2
Red-throated Loon	2	2	42	3	23	16
	2*	1	10	-	6	4
	1	1	6	-	3	3

* Includes clutches in which one egg was lost or infertile.

A pair of loons had the same chance of raising at least one young regardless of whether it started with a brood of one or two. The presence of the second young in a brood had no effect on the survival of the other young.

The second young survived in 8 of 31 broods hatching two young Arctic Loons. This yielded an average of 1.19 young per nest hatching two chicks versus 0.77 young per one-young clutches. Three of 42 Red-throated Loon broods of two raised both young for an average of 0.69 young per brood of two and an average of 0.56 young per brood of one.

Difference in success between initial brood sizes of one and two was due to the second young surviving in the broods of two.

V.G. Differential Survival of Young Arctic and Red-throated Loons

Table 67 presents the overall survival data for loon chicks on the main study area. It includes a few nests (6 Arctic and 1 Red-throated Loon) for which the exact clutch sizes or initial brood sizes were unknown. This accounts for the slightly higher totals in this table than in table 66.

Young Arctic Loons had a significantly higher survival than did Red-throated Loons at the McConnell River ($\chi^2 = 10.61$; $df = 1$; $P<0.005$).

The overall mortality can be partitioned into two components. First, to what extent was the differential survival of the two species due to greater survival of the second young

TABLE 67

OVERALL SURVIVAL OF YOUNG ARCTIC AND RED-THROATED LOONS

(POOLED 1967-68-69)

Species	Number of chicks which		Total
	survive	did not survive	
Arctic Loon	56	34	90
Red-throated Loon	39	62	101
Total	95	96	191

in Arctic Loon clutches? Table 68 indicates that Arctic Loons were more likely to raise two young than were Red-throated Loons ($\chi^2 = 4.85$; df = 1; $P<0.05$). Second, did an Arctic Loon pair have a greater chance of raising at least one young than did a Red-throated Loon pair? Table 69 shows that Arctic Loons had a greater chance of raising at least one young ($\chi^2 = 9.82$; df = 1; $P<0.005$) from nests which hatched at least one egg. The greater success of Arctic Loons was due to better survival of the first young in each nest as well as to increased survival of the second young in nests hatching two eggs.

TABLE 68

NUMBER OF PAIRS HATCHING TWO YOUNG AND RAISING BOTH YOUNG (POOLED 1967-68-69)

Species	Number of nests which hatched two young		
	Two young raised	Two young not raised	Total
Arctic Loon	8	23	31
Red-throated Loon	3	39	42
Total	11	62	73

TABLE 69

NUMBER OF LOON PAIRS RAISING AT LEAST ONE YOUNG

(POOLED 1967-68-69)

Species	Number of nests raising		Totals
	at least one young	no young	
Arctic Loon	46	7	53
Red-throated Loon	35	23	58
Totals	81	30	111

DISCUSSION

Habitat Selection

Habitat selection by birds is a poorly understood process. It apparently occurs on two levels (Lack 1949; Svardson 1949; Hilden 1965; Klopfer and Hailman 1965). There is an ultimate evolutionary level where selection for certain habitats is reflected in differential reproductive rates. This level includes such processes as competition and ecological isolation (Lack 1949, 1971). The proximate level includes the "immediately operative factors that assure the choice of the proper habitat" (Klopfer and Hailman 1965: 281). These proximate factors may or may not be the same as those factors which are important at the evolutionary level. Klopfer and Hailman (op. cit.) suggest two important questions at the proximate level. What elements of the habitat are recognized by the animal and how are they constrained to conduct the bulk of their activities in these elements?

The principal proximate factor used by the loons was pond size. Each species selected ponds of a specific size range. The primary bases for these selections were probably innate (Svardson 1949; Hilden 1965) although there may also have been an important learning component (Miller 1942; Klopfer and Hailman 1965). Are these components of habitat recognition sufficient to ensure the complete habitat

separation of Arctic and Red-throated Loons or do the species also interact where ponds are intermediate in size? The critical evidence must come from an area where one of the species occurs in the absence of the other.

Red-throated Loons used only slightly larger nest ponds on the mainland at Harrington Harbour, where Arctic Loons were absent, than they used at the McConnell River. However, they did not use larger ponds on the preferred off-shore areas at Harrington Harbour. At the McConnell River most of the intermediate sized ponds (0.8 to 1.5 ha) were occupied by Arctic Loons and were unavailable to Red-throated Loons. Red-throated Loons nesting on larger than average ponds were apt to have more interspecific confrontations with Arctic Loons than those on smaller ponds. Red-throated Loons often lost these encounters. Arctic Loons reacted faster and more violently to Red-throated Loons which intruded onto their territory than they did to intruding conspecifics. This was clearly not a case of mistaken identity but was a definite behaviour pattern. These facts indicate that interspecific behaviour restricted the use of intermediate sized ponds by Red-throated Loons but the primary habitat separation was maintained by innate preferences (possibly including a learning component). These proximate preferences explain how the habitat was divided but they do not explain why it was divided.

The evolutionary (ultimate) aspects of habitat selec-

tion are implicit in many of the important concepts of population ecology. These interrelated concepts include the theory of the niche (Hutchinson 1958; MacArthur 1968; MacNaughton and Wolf 1970), competition (Crombie 1947; Birch 1957; Orians and Collier 1963; DeBach 1966; Miller 1967, 1968, 1969; Morse 1967, 1971; Ayala 1968, 1970, 1971 and many others), character displacement and character divergence (Brown and Wilson 1956; Lack 1947; MacArthur and Levins 1964), species diversity (MacArthur 1958, 1964, 1965; MacArthur et al. 1966; MacArthur and Wilson 1967; Hutchinson 1959; Cody 1968; Keast 1968; Wiens 1969; Slobodkin and Sanders 1969; Power 1971 and others), interspecific territory (Simmons 1951; Lanyon 1957; Johnson 1963; Orians and Willson 1964; Murray 1971), and ecological isolation (reviewed by Lack 1971). Rather than review the voluminous literature on these concepts, I will attempt to elucidate which are relevant to the evolution of habitat segregation between the two loon species.

The evolution of the use of small nest ponds by Red-throated Loons is the interesting question. Arctic Loons used ponds and territories which were large enough to provide food for at least their young but why did Red-throated Loons use such small ponds which supplied no food? Mammalian predation was an important selective force influencing the distribution of Red-throated Loons at Harrington Harbour and the use of extra ponds in territories at the McConnell River.

It seems logical that the use of larger ponds by Red-throated Loons would have further reduced predation as well as supplying a potential food source. What counter-selective forces favour the use of small ponds by Red-throated Loons?

In the high Arctic the potential breeding season is very short and adaptations which maximize the time available for the nest cycle are probably highly selected. The first ponds to thaw at high latitudes are small and shallow (Johnsen 1953:18) whereas the larger, deeper ponds thaw much later (Saville pers. comm.). The use of small ponds by Red-throated Loons is an adaptation which takes advantage of this phenomenon and it is reflected in the range of the species. The Red-throated Loon breeds further north than any other species of loon (Palmer 1962; Godfrey 1966; Dement'ev et al. 1968). The use of the sea for food is a further adaptation to high latitudes, as many salt-water areas remain ice-free or at least have open leads sufficient for a feeding loon.

The present distribution and habitat of Red-throated Loons is most simply explained by allopatric speciation. The Pleistocene ice sheets were potent isolating factors affecting the speciation and distribution of animals (Mayr 1963; Mengel 1970). Ploeger (1968) presents evidence about the several arctic refugia which remained ice-free.

Sibley (1960) and Mayr and Short (1970) indicate that the Red-throated Loon is most closely related to the Arctic Loon. During the ice-ages the ancestor of the Red-throated

and Arctic Loon was probably isolated into two populations. One population occupied a cold arctic refugium and the other occurred south of the ice, in a warmer climate. Johansen (1963) considers the Arctic Loon to be a sub-arctic rather than an arctic species. The two isolated populations may then have diverged with the Red-throated Loon becoming adapted to the fast thawing small ponds in their cold refugium. When the two populations came into secondary contact they behaved as full species with different habitat preferences. These preferences were reinforced by the interspecific territories which partially restricted the use of larger ponds by Red-throated Loons. However, the main habitat differences were likely primarily adaptations to different environments rather than to competition between the species.

Arctic Loons are considered to be two species (G. arctica and G. pacifica) by Vaurie (1965) or two main races (Palmer 1962): a Eurasian one divided into G. a. arctica and G. a. viridigularis and a North American one, G. a. pacifica. Whether these populations are species, races or a superspecies (Mayr and Short 1970) is beyond the scope of this study but it is clear that the two continental Arctic Loon populations have partially diverged through isolation and this isolation probably occurred after the period when the Red-throated Loon diverged from the common ancestor. G. stellata was present in Europe during the Pleistocene (Brodkorb 1953) and G. arctica was present in California

during the late Pleistocene (Wetmore 1956). Neither species has been recorded from pre-Pleistocene deposits (Storer 1956).

Miller (1969:69) has pointed out that there is "no way that any existing model can distinguish between complete niche differentiation and competitive exclusion." The present data for Arctic and Red-throated Loons indicate that niche differentiation was the primary means of ecological isolation and competition for intermediate ponds played a lesser role. Red-throated Loons were committed to the small ponds through their structure and behaviour which placed them at a competitive disadvantage against Arctic Loons, on the larger and deeper water areas.

Territory in Loons

Howard (1920) first recognized the general importance of territoriality in birds. His book initiated a continuing controversy about the function of territory (Nice 1941; Hinde 1956; Tinbergen 1957; Wynne-Edwards 1962; Lack 1954, 1966). Brown (1964) and Brown and Orians (1970) point out that territorial behaviour does not evolve because it has a function. It is favoured if those individuals acting in a territorial manner are more successful at producing young to breeding age than are non-territorial individuals (Carrick 1963). Thus, the common denominator underlying all the diverse types of territorial behaviour is the increased success of territorial individuals or rather the reduced

success of non-territorial ones. This approach is an important breakthrough in the analysis of territory.

Territorial behaviour occurs in some form in virtually all species of birds which have been studied. This fact has led to the search for a unitary function for the behaviour. It would have been better to look for an underlying principle which could explain the appearance of territorial behaviour in so many species. Tinbergen (1956, 1957) stressed that territory involves both site-attachment and hostility (intraspecific in this case). This hostility or aggressive behaviour is probably the common factor underlying all territorial behaviour. The extension of the hostility involved in the concept of 'individual distance' may have been the precursor of territorial behaviour (Condor 1949; Marler 1956).

The factors which have been proposed as 'functions' of territory can be analyzed to see how each affects the net recruitment (i.e. number of young reared to breeding age) to a population of loons. Do any of these factors provide advantages to territorial loons which would not be available to non-territorial individuals? Territorial behaviour could simultaneously reduce mortality from several factors such as failure to establish a pair bond, predation on eggs, and starvation of young. Moreover, selection may initially favour a territorial system which reduces one mortality factor then the system may further adapt to counteract another mortality agent.

The list of possible selective advantages accruing to territorial individuals includes the following (Hinde 1956): reduction of disease and parasitism (no evidence for loons); assistance in formation and maintenance of a pair-bond; reduction of interference with reproductive activities; defense of a nest site; reduction of predation; defense of an adequate food supply; and the regulation and limitation of population density including breeding dispersion (Huxley and Fisher 1964; Tinbergen 1957). These potential advantages will be examined in terms of their effects on the fitness of territorial Arctic and Red-throated Loons.

Many authors (see Hinde 1956) have suggested that territory facilitates the formation and maintenance of the pair-bond. Loons were paired when they arrived on the breeding grounds but territory could have enhanced the maintenance of the bond. It is not evident why territories of two or more ponds were necessary to insure continuation of the pair-bond when one pond would have been sufficient. This factor does not explain the present territorial system of loons.

The holding of territory undoubtedly reduces interference with reproductive activities of the pair and this may have selectively favoured the evolution of territorial behaviour. There are several instances of intraspecific interference affecting the reproductive cycle (Armstrong 1965:278; Hinde 1956) but the significance in terms of

nesting success has not been established. Loon territories may reduce strife but again it is hard to see why a territory should consist of more than one pond when only one would be needed to reduce this interference.

The defense of a nest site is particularly important in species which use sites which are in short supply (Kluijver 1951; Hinde 1956) but other factors are important when sites are plentiful (Tompa 1967). There was no shortage of nest sites for the Arctic and Red-throated Loons at the McConnell River.

It has been postulated that territorial behaviour effects a reduction in predation on a species (Hinde 1956; Lack 1966, 1968). Territories are dispersed in a habitat and this may reduce predation through the spacing of nests (Tinbergen et al. 1967; Croze 1970; Krebs 1970, 1971). Dispersion of nests may keep the population below a level which makes it profitable for a predator to concentrate on the species. Spacing of nests may increase survival of loon nests but there was no firm evidence to support or reject this hypothesis. It was noted that Arctic Foxes spent a lot of time in areas where birds' eggs (Blue Goose) were concentrated and congregated loon nests might have suffered higher predation.

Mammalian predation was probably important in the evolution of the Red-throated Loon territorial system even if it did not act through nest dispersion. Red-throated Loons

averaged 2.86 ponds per territory at the McConnell River. The non-nest ponds in these territories were used for escape by the adults when they were threatened by predatory mammals. At Harrington Harbour, Red-throated Loon territories often had no escape pond as such but the sea was so close that escape ponds were unnecessary. It was also shown that fox predation had a profound effect on the areas at Harrington Harbour which were suitable for territories in the first place (section III). The importance of potential mammalian predation was further illustrated by the strong preference of both species for nesting on 'island-type' substrates (sections I.1.B and I.2.B) at the McConnell River.

Territories are often assumed to have an important function in supplying food for the adults and young. There has been much controversy about the relationship, if any, between territory size and food supply (Lack 1954, 1966; Hinde 1956; Wynne-Edwards 1962; Crook 1965; Schoener 1968; Watson and Moss 1970). A protected food source could lead to higher survival of territory holders. Many studies have shown that food supply and territory size are negatively correlated (Kluijver 1951; Lockie 1955a; Pitelka et al. 1955; Stenger 1958; Schoener 1968; Rowan 1969; Holmes 1970; Miller et al. 1970) although the pattern of territory utilization may vary throughout the nesting cycle (Barlow 1962; Stefanski 1967; Root 1969; Yarrow 1970; and Ricklefs 1971). The loons at the McConnell River provided a

pertinent comparison with respect to the food value of territories.

Red-throated Loons gathered no food on their territory, whereas Arctic Loon territories provided most of the food for the young. The territories of both species were interspersed and the breeding ecologies of each species were very similar so that external agents such as predators should affect each species equally. Differential adaptations of territory size may be attributable to the use or non-use of territories for food for the young.

Arctic Loons selected territories of a certain size regardless of the number of individual ponds required to ensure this size. There was no correlation between territory size and number of ponds per territory (section II.1.C). On the other hand the size of Red-throated Loon territories was correlated with the number of individual ponds per territory (II.2.B), suggesting that they selected the number of ponds rather than area. This result is explained by the hypothesis that Red-throated Loons selected for escape ponds and Arctic Loons selected for the food value of the territory.

Further evidence that territory size was important to Arctic Loons was supplied by two other trends. First, smaller territories were used less often and the birds using them were less successful than those on larger territories (II.1.C). Second, on parts of their range Arctic Loons gather all their food (for adults and young) on the nest

pond. In these areas the average territory size was much larger (in Sweden - mean = 212 ha, N = 16 - Lindberg 1968; in Finland - 100 to 150 ha - Lehtonen 1970) than at the McConnell River where only the food for the young came from the territory. Clearly, the presence of food on Arctic Loon territories was important whereas the presence of escape ponds was vital for Red-throated Loons. These factors are the prime reasons for the present territory structure of the two species.

Territory and Population Regulation

It has been claimed that territorial systems evolved to prevent populations from over-exploiting their food resources (Wynne-Edwards 1962, 1971). This view has attracted much criticism (Crook 1965; Williams 1966; Wiens 1966; Lack 1966) primarily because Wynne-Edwards invoked the controversial process of group-selection to explain the evolution of these systems. The evolution of territory can be explained by the processes of natural selection acting on individuals (including kin selection) (Brown and Orians 1970). Natural selection favouring territorial individuals can lead to a territorial system which can limit or regulate a breeding population. The regulatory effect of territory has been examined in several recent studies (Fretwell and Lucas 1969; Brown 1969a, 1969b; Brown and Orians 1970; Watson and Moss 1970, 1971; Krebs 1971).

Brown (1969a) recognized three critical levels of population density according to the presumed effects of territoriality on patterns of dispersion. At Level 1 territorial behaviour assures a mosaic pattern of dispersion but the population is not sufficently dense to deter any individuals from breeding in their preferred habitat. At Level 3 all possible breeding habitats are occupied and a surplus of potential breeders exists as non-breeding floaters. Brown (1969a) reviewed these cases and Young (1970) and Harris (1970) have provided further information on Level 3.

The level 2 density (Brown 1969a) occurs when the preferred habitat is fully used and some birds are dissuaded from breeding there by the territorial behaviour of the residents. These birds then settle in other, presumably less productive habitats.

The effects of Level 2 density have become widely accepted. Unfortunately, this acceptance is based on several studies which are, at best, only suggestive of Level 2 density effects. Therefore, it is worthwhile investigating the pitfalls of these studies in some detail before examining whether these density effects occur in the loons at the McConnell River. Krebs' (1971) recent study provides the first conclusive demonstration of Level 2 density effects.

Two conditions must be met before Level 2 density can operate. Reproductive success must be higher in the preferred areas and it must be shown that birds in the less suitable

habitat are there because they could not establish in the preferred area, rather than due to habitat selection for the less suitable area. The latter point requires that birds entering the breeding population at least attempt to settle in the preferred area. It implies that the preferred areas should be filled before the poorer areas are occupied, but the effects of familiarity and experience in previous territories should be considered. Level 2 density also requires that there be a minimum territory size beyond which territories cannot be further compressed. However, this minimum size need not be the same in different areas or even in the same area in successive years (Watson and Moss 1971). The requirement that reproductive success be higher in preferred habitats must be carefully interpreted. It is the net rate of recruitment to the breeding population and this includes the survival of the current breeders (Fretwell 1968, 1969a).

Kluyver and Tinbergen (1953) first suggested the existence of the Level 2 density effect and called it the "buffer mechanism". They showed that breeding density of Great Tits was higher and more stable in mixed woods than in pinewoods which had a poorer food supply, suggesting (no direct evidence) that the richer areas were settled first and the poorer ones later. They did show that individuals were exposed to both habitats and in fact some young raised in each habitat settled in the opposite habitats (Kluijver 1951). The proportion of young raised in pinewoods and settling in

mixed woods was significantly higher than the proportion of those raised in mixed woods but settling in pinewoods ($P<0.001$ based on analysis of data from Kluijver 1951: 95,98). This result was to be expected if the mixed wood was preferred. Brown (1969b) pointed out that Kluijver (1951) claimed that there was no difference in gross reproduction per pair of Great Tits in the mixed and pinewoods. Thus, this was not an example of Level 2 density but was merely a case of dispersion among equally productive habitats (i.e. Level 1). Unfortunately Kluijver's data are confusing. Brown (1969b) quotes Kluijver (1951: 90) to the effect that gross reproduction was 7.1 young per pair in the pinewood and 6.8 in the mixed wood. On the same page (90) Kluijver states that the average production on the Oranje Nassau's Oord (O.N.O) study area was 7.6 young per pair for the period 1922-33, and 7.3 for the following 11 years. He later states (p. 119) that the average production rate on O.N.O. was 7.4 young per pair but he did not say for what period. All three of these average figures are higher than those quoted by Brown which apparently refer to several mixed and pine-woods and not just the ones under study. Kluijver (1951:90) also stated that "for 22 years at O.N.O. the annual differences in production rates were in no case statistically significant". This implies that annual differences between habitats, were tested rather than the overall data. If there was a buffer mechanism it must have evolved over a fairly long period of

time and there need not be significant differences in reproduction between areas in any one year as long as the overall fitness varies over a period of time. The data presented by Kluyver and Tinbergen (1953) can neither prove nor disprove the existence of Level 2 density effects.

Glas (1960) found that Chaffinch (Fringilla coelebs) population levels were more stable in high density areas (mixed woods) than in areas with low density (pinewoods). He also found that Chaffinches started to settle in the pinewoods at least 13 days later than in the mixed woods. These results indicated a preference for mixed woods but he did not examine success in the two habitats in spite of what Brown and Orians (1970:250) claim.

Delius (1965) has shown that Skylarks (Alauda arvensis) normally occupied marginal areas at low densities but were absent when population levels in preferred areas were below normal. Tompa (1962) showed that Song Sparrows (Melospiza melodia) emigrated from areas of high breeding density to ones of low density. Williamson (1969) found that certain habitat types were preferred by Wrens (T. troglodytes) which were recovering from severe winter mortality. As the population increased, secondary and tertiary habitats were occupied. Territory size remained the same during the periods of low and high populations. These studies show that species have preferred habitats and they are suggestive of Level 2 density effects but they did not examine all the relevant factors.

Ficken and Ficken (1967) found that yearling American Redstarts (Setophaga ruticilla) occupied suboptimal habitat and had lower success than adult birds. The yearlings arrived on the breeding grounds later than the adults and were less aggressive. The Fickens imply that territorial behaviour by the adults kept the yearlings from the preferred area.

Zimmerman (1971) showed that Dickcissels (Spiza americana) had a minimum territory size and when the population increased males were forced into sub-optimal habitat where they attracted fewer mates. This was first suggested by Fretwell and Calver (1969).

The best evidence for the effects of Level 2 density comes from Krebs' (1971) study of Great Tits. He found that birds which nested in sub-optimal hedgerow territories were less productive than those in wooded areas. When territory holders were removed from the woods, they were replaced by hedgerow birds. The hedgerow birds were mostly yearlings and were not replaced when they moved into the woods. The hedgerow birds were originally kept out of the woods by the territorial behaviour of the residents.

Clearly, there is only a limited amount of information on the effects of Level 2 density on local bird populations. The Red-throated Loon provides clear-cut evidence for the effects of this density level.

There was potentially strong selection favouring Red-

throated Loons which nested close to the coast of Hudson Bay. Pairs nesting near the coast spent less time flying to the feeding grounds. The air speed of Red-throated Loons on feeding flights was 75 kph or 1.25 km per minute (Davis 1971). Thus, a pair nesting 20 km from the coastal feeding grounds and making 15 feeding trips per day would spend 8 hours in the air (600 km). Ten feeding trips (400 km) would require 5.3 hours. This represents a significant amount of time during which the adults were not searching for fish and it also would require a significant energy outlay. A pair nesting 5 km from the coast could make 15 feedings trips with only 2 hours flying time.

Red-throated Loon habitat was a continuous gradient of suitability based on distance from the coastal food sources. Areas close to the coast were more suitable and the Red-throated Loons responded by occupying them in much higher densities than inland areas. The breeding density declined significantly as distance from the coast increased (section III). This raises the question of why all pairs did not nest near the coast?

The answer was that the territorial behaviour of the resident pairs forced other pairs to nest further inland. The average territory of Red-throated Loons consisted of 2.86 ponds and this did not vary throughout the main study area (section II.2.B). Nesting pairs used the same sized territories in all areas regardless of breeding density which suggests that this size represents a minimum beyond which

territorial behaviour prevents further compression.

Another condition necessary for Level 2 density was that birds nesting in sub-optimal habitat were at least exposed to the better habitats and this was certainly true for this population of Red-throated Loons where any loon flying to the coast had to pass over the best habitat. Loon territories were selected over a period of several weeks during the late summer and thus it was not possible to tell in which order they were actually chosen (Appendix 1).

The final critical point is whether the pairs in the less dense breeding areas were actually producing fewer recruits to the breeding population. It was not possible to examine the survival of young beyond five to six weeks of age but there was no reason to suspect that fledglings from the less dense inland areas would ever have a higher survival rate after they left the breeding grounds. There was no significant difference in the mean clutch size in the four sub-divisions of the main study area. In view of the small sample sizes the two inland sub-divisions (C and D in figure 2) were grouped into one area with a mid-point 13 km from the low tideline of Hudson Bay. The two coastal areas were also pooled (A and B of figure 2) with a mid-point distance of 9.5 km from the low tideline. The number of young produced per nest in which the eggs successfully hatched was examined. Figure 11 shows the difference (in the average number of young surviving per nest) between the coastal

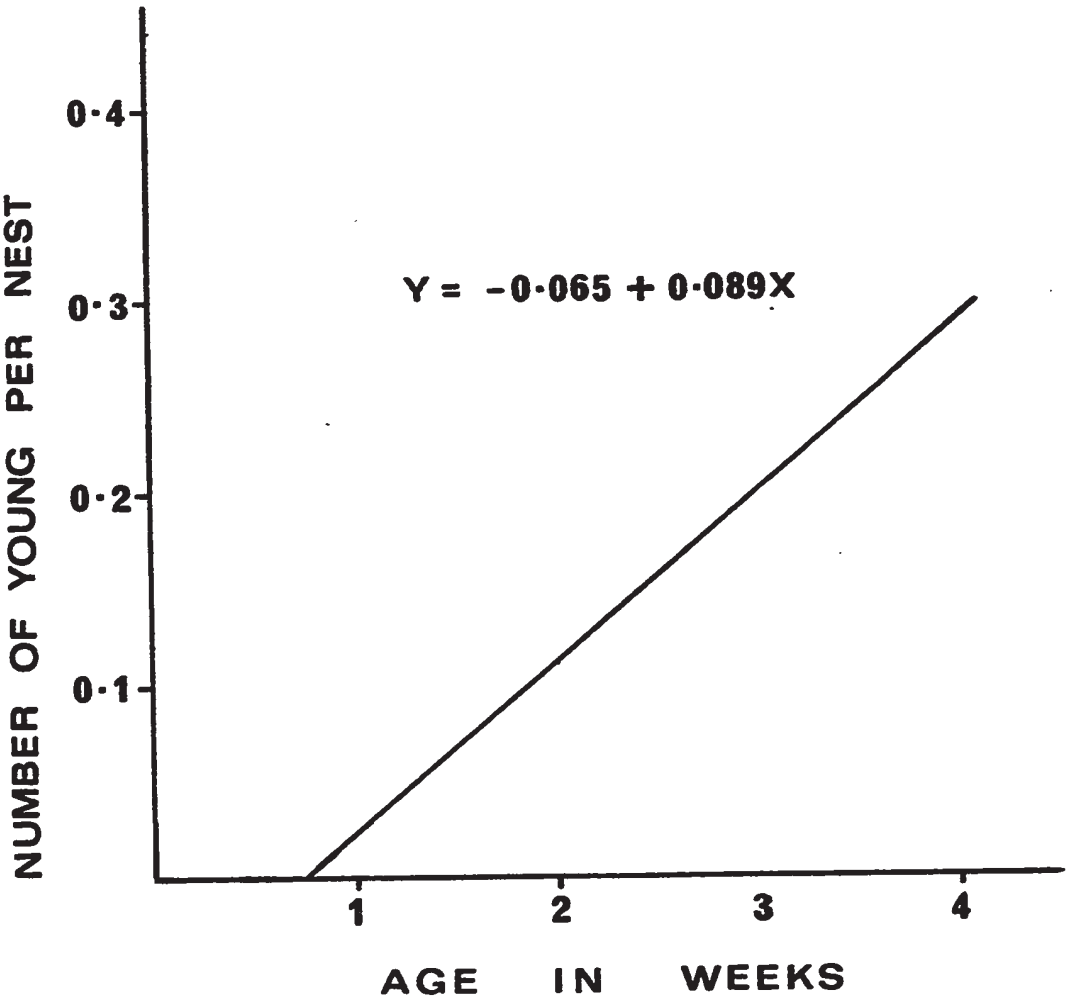

Figure 11. Differences in the number of surviving young Red-throated Loons per brood in coastal versus inland study areas. Data expressed as the regression of differences in the two areas as a function of time since hatching. Data pooled for 1967-68-69 at the McConnell River.

(A and B) and inland (C and D) areas. The differences increased in a significant linear regression on age in weeks ($F = 38.27$; $df = 1, 2$; $P<0.03$). The coastal areas were more successful.

At four weeks of age, 17 of 48 nests in the coastal areas still had living young whereas only 5 of 34 inland nests still had living young. These rates were significantly different ($\chi^2 = 4.35$; $df = 1$; $P<0.05$) and indicated that birds in the low density inland areas were less successful than those in the coastal areas. All three pairs of Red-throated Loons which raised two young to four weeks of age nested in the coastal areas.

The data for Red-throated Loons clearly indicated that Level 2 density existed and that territorial behaviour was regulating the population level by forcing some pairs to breed in less suitable habitats and produce fewer young. This does not necessarily mean that territory was limiting the population. Birds nesting in the inland areas were more successful than if they had not nested at all and in this respect it can be said that territory was maximizing the population. However, it is not known what the success rate would have been for these birds if they had squeezed into the primary area and thereby lowered the territory size of all birds in that area. This might have resulted in a density-dependent reduction of the reproductive rates (Brown 1969b).

The system of territory in Arctic Loons was basically

similar to that of Red-throated Loons. The fact that young Arctic Loons were fed from the nest pond meant that selection acting through distance from the coast depended upon food for adults rather than food for young and the decrease in breeding density occurred further inland for Arctic Loons than for Red-throated Loons. There was no decrease in Arctic Loon density on the main study area. The low density areas were not intensively studied and no data were collected on reproductive success in them. Arctic Loon habitat was fully occupied and additional pairs were forced to nest in areas further from the coast. If Arctic Loons had used only one pond per territory then more pairs could have nested in the good areas. The potential newcomers were dissuaded by lack of undefended habitat rather than an absolute lack of habitat.

Ecology of Growth

Laird (1965), Laird and Howard (1967), and Laird et al. (1968) have analyzed the mathematical aspects of animal growth curves. They have also discussed in detail the dynamics of the relative growth rates of different parts of the animal. It remained for Ricklefs (1968, 1969) and Lack (1968) to stress the importance of the comparative approach to the study of avian growth patterns and their adaptive nature. Ricklefs' extensive review (1968) was based on weight increases and was only suggestive of the integrated pattern of total growth. Ricklefs (1967), Holcomb (1968) and Holcomb

and Twiest (1968) correlated differential growth rates of structures of passerines with their function in the nesting ecology of the species, and Brown and Amadon (1968:113) made similar observations on the Falconiformes. None of these studies has fully investigated the ecological strategy adopted by the young of a particular species.

The growth data for Red-throated Loons (section IV.1.C) illustrated the complex nature and interaction of these adaptations. The differential growth was probably adaptive and increased the survival of the individual young.

It was shown (section IV.2) that in most cases the younger chick of a brood starved to death. In spite of this, one parent stayed on the nest pond until the young were nearly two weeks old when they were large enough to protect themselves from gulls. If both adults had fed the young then more food would have been available to the young but this would have jeopardized the older young, through predation. Thus, growth and behaviour patterns combined to protect the older young of a brood even though the younger brood member may have been starving. These patterns must have affected the distance from coastal food sources at which Red-throated Loons could nest.

Significance of Asynchronous Hatching

Lack (1954:40) believed that asynchronous hatching "is almost certainly a valuable adaptation". "There is in fact, every reason to suppose that the habit of starting

incubation before the clutch is complete, and the consequent difference in the size of the young in the early stages, is an adaptation for bringing the family-size into closer adjustment with the food supply" (Lack 1954:41). This phenomenon is of potential importance for species in which the parents feed the young.

The widespread occurrence of species exhibiting asynchronous hatching and the resulting differential mortality of the young is not generally realized. These species include members of the following groups: penguins - Spheniscidae (Gwynn 1953; Richdale 1957), boobies - Sulidae (Dorward 1962; Nelson 1966c; Simmons 1967, 1970; Kepler 1969), cormorants - Phalacrocoracidae (Lack 1968:245), herons - Ardeidae (Owen 1960; Jenni 1969; Dusi and Dusi 1970), storks - Ciconiidae (Lack 1966:223; Kahl 1966), waterfowl - Anatidae (Davies 1963; Lowe 1966; Kear 1970); hawks - Falconiformes (Ingram 1959; Brown and Amadon 1968; Hamerstrom 1969; Scharf and Balfour 1971), oystercatchers - Haematopodidae (Safriel in Kear 1970), jaegers - Stercorariidae (Saville and Oliver 1964; Maher 1970; Spellerberg 1971), gulls - Laridae (Coulson and White 1958a), owls - Strigiformes (Watson 1957; Lack 1966:274; Southern 1970), swifts - Apodidae (Lack and Lack 1951), woodpeckers - Picidae (Ligon 1970), crows - Corvidae (Lockie 1955b), titmice - Paridae (Gibb 1950; Dhondt 1970), thrashers - Mimidae (Ricklefs 1965); thrushes - Turdidae (Snow 1958; Tyrvainen

1969), shrikes - Laniidae (Cade 1967), starlings - Sturnidae (Dunnet 1955), blackbirds - Icteridae (Selander 1960; Orians 1961), weaverbirds - Ploceidae (Ward 1965; Seel 1968, 1970) and some hole-nesting passerines (Lohrl 1968).

Certain general patterns are found in these studies. The parents feed their young in all cases. This includes two anatids (Anseranas and Biziura) in which the young do not feed themselves. In cases where the food supply has been examined it was apparently variable and unpredictable (Simmons 1967, 1970; Owen 1960; Brown and Amadon 1968; Lack and Lack 1951; Southern 1970; Lockie 1955a; Orians 1961; Ricklefs 1965). Asynchronous hatching was an adaptation adjusting brood-size to a fluctuating food supply.

Several hatching patterns are found. Many species such as the Snowy Owl (Nyctea scandiaca) began incubation with the first egg and the young hatched at regular 38-48 hour intervals (Watson 1957). Hatching was staggered in the Red-cockaded Woodpecker (Dendrocopos borealis) with the first two eggs hatching together followed by the next two at 12 hour intervals (Ligon 1970). In Passer domesticus all eggs in two and three egg clutches hatch synchronously but in larger clutches the last egg hatched later (Seel 1968). The Great Tit had synchronous hatching in early broods but last eggs hatched asynchronously in late nests (Gibb 1950).

The efficiency of systems based on asynchronous hatch-

ing was variable. In the Swift (Apus apus) clutches of one, two and three eggs were equally successful in years of food shortage and the surplus young did not affect the outcome of the first hatched (Lack and Lack 1951). However, the fourth young of the Grey Heron (Ardea cinerea) broods depressed the growth rate of the third young and thus both were jeopardized although the older two were not (Owen 1960).

The disappearance of last hatched young was usually due to starvation or other mortality due to weakened condition caused by lack of food. These related causes include eviction from the nest and fratricide. Ingram (1959) reviewed juvenile cannibalism in 17 species of hawks and 5 owls but the fratricide was probably based on the weak condition of the victims although Ingram (1959), Wynne-Edwards (1962) and Skutch (1967) did not think that nutrition was a factor.

In the cases of differential mortality due to asynchronous hatching reviewed above, the mortality was due to differential food intakes by the brood members. The competition between young was based on the size and strength of first hatched young. The young which gaped the widest, begged the loudest, and reached the furthest were fed by the parents. When large young were satiated the rest then had a chance to feed. The hierarchy was apparently based on a straightforward struggle for food. Kear (1970) suggests that a dominance hierarchy exists in the nidifugous young of

Magpie-geese (Anseranas semipalmata) and Oystercatchers (Haematopus ostralegus) and that survival of young is based on status in the social hierarchy which in turn depends on age of brood members. There are interesting similarities to the nidifugous broods of loons.

There was nothing inherently wrong with those young which perished in the face of competition from older siblings. When the competition was reduced, either by increasing the food supply or by removing competitors, the formerly doomed young were able to grow normally and survive (Lack and Lack 1951; Gwynn 1953; Ricklefs 1965; Simmons 1967; Lohrl 1968; Kepler 1969; Ligon 1970; Spellerberg 1971).

The subtlety of nestling survival patterns was illustrated by Dhondt (1970). Male Great Tits were larger than females even as nestlings and in areas of food shortage significantly fewer females fledged. In areas with sufficient food the sexes fledged equally well. The slightly larger size of the males was sufficient to insure better survival when food was short. In species with asynchronous hatching and sexual size dimorphism it was found that hatching sequence overcame size differences due to sex (Selander 1960; Scharf and Balfour 1971) but Cave (1968) found that female nestling Kestrels (Falco tinnunculus) survived better than the smaller male nestlings, when food was short.

The Red-throated Loon has evolved an elaborate system for adjusting brood size to available food sources. The first

hatched young survived and grew better than its sibling unless sufficient food was available in which case both young survived. The first hatched chick was fed first due to its dominance over its broodmate. The second hatched, although slowly starving, remained subordinate and did not challenge the older chick. The younger chick received most of its food when the older chick was full and the presence of the second young had no adverse effects on the growth (weight, culmen, or tarsus) or survival of the first hatched Red-throated Loon chick. The data for Arctic Loons indicated that they had developed a similar method of brood regulation.

The system is a remarkably efficient use of energy which insured that one young was successful before energy was diverted to the second young. This energy distribution was accomplished with a minimum of interbrood strife. The loons are an example of the refinement which is possible in a system of brood regulation based on immediately available food supply.

The widespread occurrence and adaptive significance of asynchronous hatching have not been properly stressed in the major reviews of avian clutch-size (Lack 1954, 1966; Wynne-Edwards 1962; Skutch 1967; Klomp 1970). It is an important factor in the evolution of clutch size. The system actually adjusts brood-size to food supply (Lack 1954; Ricklefs 1965).

Laying Interval

Lack (1968:291) postulated that the interval between the laying of successive eggs in a clutch was determined by predation and food available to the laying female. Predation pressure on eggs tends to reduce the interval between successive eggs and thus shortens the period when eggs are susceptible to predation. Opposed to predation he suggested that the females of some species were unable to collect enough food to lay every day and this resulted in the longer laying intervals found in several species. This was undoubtedly true for the Swift which Lack found to have a variable laying interval depending on food availability (Lack 1956). However, the long laying intervals (2 or more days) of many species cannot be easily explained by Lack's hypothesis. There is often no evidence that food supply is short for the female and many species apparently show no correlation between length of laying interval and food supply.

Species laying large eggs may be expected to have longer laying intervals as greater food reserves are necessary for each egg. However, there was no correlation between egg-size (relative to adult body weight) and length of laying interval in cursorial birds and several seabird families (Lack 1968:210, 243). Another explanation for long laying intervals must be found and the Arctic and Red-throated Loon provide it.

The eggs of the loons were relatively small (5.3% of

adult weight for Red-throated Loons and 4.8% for Arctic Loons - data for eggs from section V.2 and weight from table 21). The total energy required for the clutch of these species (clutch size X relative size of egg) was not overly large (10.6% for Red-throated Loons and 9.6% for Arctic Loons). This energy drain was much less than that of a host of species, many of which lay daily (data from Lack 1968). Ryder (1970) and Hanson (1962) have shown that arctic nesting Ross Geese (Chen rossi) and Canada Geese arrive on the breeding grounds carrying the energy required for eggs. These energy stores were laid down long before actual egg-laying and illustrate the ability of birds to build-up and store energy reserves for eggs. It is not necessary for a bird to obtain all the energy for each egg during the period between laying of successive eggs.

No more than 3.5 per cent of the time which adult loons spent on the nesting territory during the pre-laying period, was spent in territorial defense (section II). Arctic Loons spent 68 per cent of their time on the territory. If food was scarce they certainly could have spent more time feeding since actual territory defense required so little time. The pattern was similar for Red-throated Loons which spent only 0.46 per cent of their total time in territorial defense during the pre-laying period.

Arctic and Red-throated Loons arrived at the Hudson Bay coast during the first week of June. They moved inland

and occupied the nesting ponds when these ponds thawed. The loons then waited until the flood receded and the natural shorelines of the nest ponds emerged as dry land. The loons then initiated nest-building and egg-laying within a day or two. This occurred in mid-June in 1967 and the last 3 days of June in 1968. Since the loons were unable to predict when the shorelines would appear above the flood waters it appeared that the loons must have been capable of laying at any time during the last 3 weeks of June. In early seasons the loons replaced lost clutches within a few days. Arctic and Red-throated Loons did not appear at all limited by food for the laying female and they were presumably capable of laying on consecutive days, if selection had favoured it.

Loons could have reduced predation on eggs by laying on consecutive days and thereby reducing the incubation period by one day. However this did not happen, which indicates that a stronger counter-selective force was acting to maintain the two day laying interval. This factor was the increased production of young due to asynchronous hatching.

The loons laid their eggs two days apart but they hatched at only one day intervals. The processes which synchronize the hatching of avian clutches have been studied by Vince (1969). Two potential synchronizing agents, calling and clicking inside the egg, were heard in both Arctic and Red-throated Loon eggs. It seems likely that if loons laid

at one day intervals then the eggs would hatch nearly simultaneously and the advantages of asynchronous hatching would be lost.

It was necessary for the loons to begin incubation with the first egg in order to protect it from predation by jaegers and gulls but this does not explain the two-day laying interval.

The data for Arctic and Red-throated Loons indicate that the two-day interval was not due to the female's inability to gather food but was necessary to insure the asynchronous hatching which was so important to the survival of young. This factor is probably important in the evolution of laying intervals in many species exhibiting asynchronous hatching.

Clutch Size in Loons

Lack (1954, 1966) postulated that natural selection has acted to maximize reproductive rates in bird species in which the adults feed the young. The upper limit to clutch size is the amount of food the adults can bring to the young. The population is then regulated by density-dependent mortality outside the breeding season. Wynne-Edwards (1962) and Skutch (1967) have counter-argued that reproductive rates are adjusted to mortality rates. This implies that some females were producing fewer recruits to the breeding population than they were capable of. Skutch observed that tropical species were not raising as many young

as they could feed. Fretwell (1969b) gave an explanation of how Lack's hypothesis could be reconciled to Skutch's data by means of "a mechanism involving dominance whereby mortality is selectively visited on excess offspring". Cody (1966) placed the problem of clutch-size in a more general theoretical framework which incorporated the existing theories of clutch-size determination in terms of the allocation of time and energy in environments of varying stability.

The clutch size of Arctic and Red-throated Loons was adjusted to be maximum number of young which the adult could feed. In fact, the loons could rarely raise more than one young, and they have evolved an elaborate system (based on asynchronous hatching) to protect this single young.

In view of the low survival of the second young, why did they persist in laying two-egg clutches (74% of Arctic Loons and 83% of Red-throated Loons laid two eggs)? The two-egg clutch must have been selectively favoured over a one-egg clutch.

There was no evidence that the laying of the second egg was a strain on the female. There was no evidence of external differences in the eggs within a two-egg clutch or between one and two-egg clutches. If the eggs were initially equal then factors subsequent to egg-laying must determine the comparative survival potential of one versus two-egg clutches.

The most obvious advantage of the second egg was the

periodic successful production of a second young. This occurred in 8 of 31 broods of Arctic Loons at the McConnell River and in 3 of 42 Red-throated Loon broods. The second young only survived when food was sufficient after the first hatched young was fed.

An interesting finding was that a two-egg clutch in both species was more likely to produce a single young than was a one-egg clutch. They were more successful even if they did not raise a second young. This was brought about by the following mechanisms.

Pairs laying two-egg clutches were less likely to lose eggs than were pairs with clutches of one egg. This difference was a function of parental care of the eggs. It is not known why such a difference occurred. It was possible that birds laying only a single egg were young, first breeders and were less skillful at protecting their eggs. This phenomenon has been observed in other birds (Coulson and White 1958b; 1961; Klomp 1970:112). It was unlikely that the age factor was important for the loons since the data indicated that females on particular territories tended to lay the same sized clutches in successive years. Evidence from this study (circumstantial) and others (Dement'ev et al. 1968) suggests that loons occupy the same territories from year to year. Clutch size might be a reflection of the condition of the female and those birds laying only one egg may not have been in good physical condition. The same birds must have been

sub-standard in most years and there was no evidence for this. It is reasonable to expect that birds nesting further from the coastal food source were more likely to suffer food shortage and hence lay a reduced clutch. However, the one-egg clutches were spread more or less uniformly throughout the study area and bore no relationship to distance from the coast. A further possibility was that two eggs provided a stronger stimulus to the incubating birds and this increased their parental care of the eggs. Tinbergen (1953b) found that an abnormally large egg provided a 'super-normal' stimulus to incubating gulls. It is possible that a clutch of two eggs provided loons with a stronger stimulus than a one-egg clutch. The whole problem of why parents with two eggs gave them better protection, requires further study.

The two-egg clutches had the further advantage that the loss of one egg increased the survival rate of the remaining egg. The increased success was apparently due to the adults learning about predators.

The two-egg clutch was advantageous, even if the second young never survived, because an egg in a two-egg clutch was more likely to produce a young than an egg in a single egg clutch. Kepler (1969) found a similar situation in the Blue-faced Booby (Sula dactylatra) which laid two eggs but never raised two young. This was true of several different populations of this species (Dorward 1962; Bartholomew 1966; Nelson 1966b; Simmons 1967). Kepler

(1969) found that the second egg conferred a significant advantage on that clutch size and increased its survival over that of one-egg clutches. This was due to the fact that 22 per cent of all young produced in two years originated from the second egg.

The two-egg clutch was advantageous for Arctic and Red-throated Loon through the occasional raising of the second young in broods of two and the better chance of hatching at least one young.

Why do Some Species Lay Only One Egg?

The two-egg clutch and asynchronous hatching were found to be an efficient system which maximized production of young Arctic and Red-throated Loons. This system was so effective that it raises the question of how any species could maximize production of young by evolving a clutch-size of one egg? There are several possible reasons for single egg clutches. These include the absolute inability of the female to gather enough energy for a second egg; the absolute inability to raise more than one young; and predator-free environments in which very few eggs were lost and a second egg provided no 'insurance effect' for the brood.

Another potential factor favouring a single egg clutch is the feeding behaviour of the parents. The nesting adults of many species make long foraging trips and this results in broods being fed at long intervals and receiving a large amount of food each time. It may not be possible for a first

hatched chick to utilize the whole large feeding without a second chick getting a significant portion of the food. A first hatched chick may not be able to ingest a complete meal in the face of competition from a second young. This could result in neither young garnering enough food to survive. However, if there were several smaller feeds throughout the day the broods could establish a stable dominance system and the older chick could assimilate the energy from each feed before the next meal is presented. Therefore, the frequency and size of feedings can have a profound effect on the clutch size of birds, particularly those with small clutch sizes.

Several species of boobies (Nelson 1966b, 1969) are adapted to irregular food supply. Two such adaptations are the ability of chicks to ingest large irregular feedings and the retention of intense begging behaviour by chicks right up to the day of death due to starvation (Nelson 1966b:455). It is possible that the large size of each feed and the strong begging by a second chick would result in part of the feed being diverted to the younger chick and this could jeopardize the first chick. Thus, it may not be possible to establish a two-egg clutch under feeding conditions characterized by large amounts of food delivered to chicks at long intervals.

Arctic and Red-throated Loon chicks are fed daily with several relatively small feedings and this allows them to establish an efficient system of raising young based on a brood of two young with a stable dominance relationship.

Productivity of Loon Populations

The two loon species at the McConnell River provided an interesting contrast in breeding success. Arctic Loons were more apt to raise at least one young in a brood and were more likely to raise the second young of a brood than were Red-throated Loons. These differences were correlated with different food sources for the young, with Arctic Loons using the nest pond and Red-throated Loons using the sea. These success rates can be reversed in some other areas.

In 1968 and 1969, Ian Newton (pers. comm.) noticed the size of nearly fledged broods on the Outher Hebrides, Scotland. There were 3 Arctic Loon broods with one young and none with two young. Three broods of Red-throated Loons had one young and nine had two young. These ratios were significantly different ($P = 0.002$ by Fisher's Exact Test for the H_o; 3:9 = 3:0). In this area the Arctic Loons fed on the large nesting lochs and the Red-throated Loons fed at sea. In Sweden, Lindberg (1968) found that 3 of 4 Arctic Loon nests hatching two young were able to raise both of them, whereas Braun et al. (1968) found that 1 of 2 young died of "malnutrition" in each of 2 nest attempts by Red-throated Loons.

Two principal factors could cause differential juvenile survival between the two species; the quantity of food available to the young and differing parental care due to location of the source of food. The Arctic Loon usually feeds its young with food gathered in the nest pond and this

means that the adults were always present with the young. On the other hand Red-throated Loons bring in food from other water areas and must leave their young. The species used these feeding regimes both at the McConnell River and the Outer Hebrides which indicates that food supply was the major factor differentiating success as the parental care was similar in both areas.

At least one adult Red-throated Loon was with the young at all times until about 13 days of age (table 40). At this time both adults began leaving the territory simultaneously. Adult Arctic Loons did not leave their young unprotected in 304 hours of observation at nesting territories. This increased protection might have conferred a slight advantage on young Arctic Loons but it would be slight since little predation of Red-throated Loon chicks occurs after they reach two weeks of age.

Food supply was apparently the most important factor affecting the differential survival of the young of the two species.

To summarize the main findings of this study, it was found that each species was adapted in slightly different ways to the simple tundra habitat. Asynchronous hatching allowed an efficient utilization of energy on a per brood basis. The system of territory fostered energetically efficient use of space on a population level. Habitat selection and reinforcing interspecific competition allowed more efficient use of the habitat on a community level.

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APPENDIX 1

TIMING OF NEST POND SELECTION

There is some circumstantial evidence that loons selected their breeding territories during the late summer prior to the breeding season. This was selectively advantageous as it reduced the time spent in territorial establishment during the spring. It allowed nesting to begin as soon as possible and thus increased the probability of raising young to fledging before the early Arctic freeze-up. Prior selection of nest areas and territory establishment in summer allowed the birds to become familiar with the nesting ponds, escape areas and feeding locations.

It is not known when young loons first return to the breeding grounds (Palmer 1962) but they evidently do not attain adult plumage until their second year. Lehtonen (1965) presented circumstantial evidence that immature Arctic Loons in Finland first took up territories at 5 or 6 years of age but did not lay eggs until the next year. Only loons in adult plumage were seen at the McConnell River.

Birds returning to the breeding grounds for the first time might do so in summer and join in the period of summer territory establishment. Lehtonen (1965) found that non-breeders returned 2-3 weeks later than the breeders and he assumed that the non-breeders were young birds. Alternately

new birds could return in the spring with the former breeders. They would then fill in territories where the previous adults had not returned to the area. In either case the main breeding population has established a stable territorial system with only minor adjustments required after spring arrival on the breeding grounds.

The return of young birds to the breeding area in years before nesting is attempted is a well documented phenomena (Richdale 1951; Lack 1956:25, 1968:299; Coulson and White 1958; Cooch 1958; Westerkov 1963; Nelson 1966a; Harris 1967; Serventy 1967; Sherwood 1967; Fisher and Fisher 1969; and others). There are also several references to the holding of territory after the main breeding effort has been concluded for the season (Falls 1969) and in seasons before first breeding (Crook 1964; Soikelli 1967; Lack 1968:299) including suggestive evidence of the latter for Arctic Loons (Lehtonen 1965).

The evidence for summer territory establishment is presented below for Arctic and Red-throated Loons.

Occupation of territory after nest loss

Loons which successfully raised young occupied their territories until the young fledged which was just before freeze-up. A high proportion of nesting loons had their eggs or young destroyed. In most cases no renest was attempted. These failed breeders fed completely on Hudson Bay and there

was no need for them to return to the nesting territories. However, the following data indicate that failed breeders spent a significant proportion of their time on territories. The data came from two sources; the analysis based on routine nest visits and observations from the towers.

The number of adults was noted on territories which had lost their eggs or young. The method is described fully in Appendix 2. The data are presented in table 70 where nests losing eggs are pooled with those losing young. The validity of this pooling procedure was tested by comparing the number of ponds with zero and two adults for territories losing eggs and those losing young (Ponds with only one adult and those where it was not known whether the eggs hatched before loss, are omitted). There was no difference in rate of pond occupation ($\chi^2 = 0.0028$; df = 1; P is NS for the H_o; 5:5 = 28:27 for Arctic Loons and $\chi^2 = 1.42$; df = 1; P is NS for the H_o; 16:11 = 18:6 for Red-throated Loons). Thus it was valid to pool all cases of nest loss for this analysis.

Table 70 shows that failed Arctic Loon pairs occupied nest ponds in 50 per cent of the cases (the 8 cases with more than 2 loons will be discussed later) and Red-throated Loons in 33 per cent of the visits.

Further data were obtained from the observation towers. These observations on undisturbed ponds were taken at least one half hour apart on any particular pond. There were 202 observations of 14 Arctic Loon territories and 108 of 8 Red-

TABLE 70

NUMBER OF ADULT LOONS PRESENT ON TERRITORIES ON WHICH EGGS OR YOUNG HAD BEEN LOST

	Number of adults present				
	0	1	2	3 or more	Total
Arctic Loon	37	3	48	8	96
Red-throated Loon	34	1	17	0	52

throated Loons territories. There was no difference between pairs which lost eggs versus those losing young ($\chi^2 = 1.05$; df = 2; P is NS for the H_o; 75:37:75 = 5:2:8 which were the number of cases with 2, 1, and 0 adults respectively for Arctic Loons). All observations on Red-throated Loons were on pairs losing their eggs.

The data for Arctic Loons were analyzed in a three-level contingency table (71) which examined the number of adults present (0, 1, or 2), time of day (08:00 to 16:00 and 16:01 to 24:00), and length of time since nest loss (1-7 days, 8-14 days, and over 14 days). The overall test of independence revealed that the three levels were not independent of each other (G = 74.42; df = 12; P<0.005). The main component of this dependence was supplied by the relationship between number of adults and time of day (G = 55.45; df = 2; P<0.005) with two adults more often being present later in the day. Two adults were present 59 per cent of the time between 16:01 and 24:00 whereas two adults were present only 12 per cent of the time between 08:00 and 16:00. The number of adults was the same for all three periods after the time of nest loss (G = 1.49: df = 4; P is NS) which indicates that the tendency of adults to return to the former nest pond did not diminish with time, after loss of the nest.

The data for Red-throated Loons (table 72) were also examined in a three-level contingency table but the time after

TABLE 71

NUMBER OF ADULT ARCTIC LOONS PRESENT ON TERRITORIES WITH FAILED NEST ATTEMPTS

Number of days since nest loss	Number of adults present	Time of day		
		08:00-16:00	16:01-24:00	Totals
0 - 7	2	4	34	48
	1	10	11	21
	0	32	11	43
	Totals	46	56	102
8 - 14	2	1	18	19
	1	7	3	10
	0	17	5	22
	Totals	25	26	51
Over 14 (up to 32)	2	5	18	23
	1	1	7	8
	0	7	11	18
	Totals	13	36	49
	Grand Totals	84	118	202

TABLE 72

NUMBER OF ADULT RED-THROATED LOONS PRESENT ON TERRITORIES WITH FAILED NEST ATTEMPTS

Number of days since nest loss	Number of adults present	Time of day		
		08:00-16:00	16:01-24:00	Totals
0 - 7	2	3	18	21
	1	3	8	11
	0	20	13	33
	Totals	26	39	65
Over 7 (up to 28)	2	3	18	21
	1	1	3	4
	0	11	7	18
	Totals	15	28	43
	Grand Totals	41	67	108

nest loss was divided into only two periods due to restricted data. The three levels were not independent of each other ($G = 26.62$; $df = 7$; $P<0.005$) largely because the number of adults depended on the time of day ($G = 16.54$; $df = 2$; $P<0.005$). Pairs of adults were more likely to be present between 16:01 and 24:00 than between 08:00 and 16:00 (54% versus 15%). The number of adults was unaffected by the passage of time since the loss of the nest ($G = 3.36$; $df = 2$; P is NS).

It was clear that both species spent a significant amount of time on territory even after eggs or young were lost and this tendency did not diminish as the season progressed (until mid-August at least).

Territory defense and roving flocks

Failed breeders defended their territories against intruders but the displays were usually not intense. The most striking feature of these territories was the common occurrence of roving flocks of adult Arctic Loons. These flocks moved from one territory to another and displayed on each. The displays were often complex with up to 12 birds posturing and lasting up to 43 minutes on one pond. The flock would then take-off and fly to another territory where displaying continued.

The average number of birds in these Arctic Loon flocks was 6.9 (range 3-12; SD = ±2.414). The flocks never landed on territories which still harboured an active pair

(with eggs or young). They moved from one unsuccessful territory to another.

The majority of flock members were failed breeders which were holding territories. This was demonstrated by a flock of 6 birds which moved to three other territories and was joined by the resident pairs of each territory until there were 12 adults in the flock.

On other occasions the flock would land on territory and the resident Arctic Loons (failed breeders) would display violently until the flock moved on.

Many authors have noted regular flocking behaviour by Arctic Loons on feeding grounds (Taverner and Sutton 1934; Witherby et al. 1941; Lehtonen 1965; Sjolander 1968; Jehl and Smith 1970). The purpose of these social gatherings is unknown. They do not seem comparable to the roving flocks at the McConnell River since they are often very regular (same time and place every day) (Sjolander 1968) and occur away from the nesting grounds.

It seems reasonable to suppose that the roving flocks at the McConnell River served to familiarize the birds with the area and with each other. The ability of birds to recognize individual conspecifics is well documented (Tinbergen 1953b; Thorpe 1961:47, 1963:427; Armstrong 1963:10, Scott 1963; Hutchison et al. 1968; Falls 1969; Beer 1970a, 1970b; Krebs 1971). This familiarity may help to solidify the territory structure of failed breeders and allow new pairs to

fit into the system.

Red-throated Loons did not exhibit such marked roving flock behaviour. Six flocks ranged from 3-6 birds (mean = 5.0). These flocks spent more time in the air, calling loudly whereas Arctic Loons just flew from pond to pond with little display on the way. There were fewer flocks of Red-throated Loons (6 per 87 hours versus 25 per 131 hours for Arctic Loons ($\chi^2 = 4.04$; df = 1; $P<0.05$).

Amount of time devoted to territory establishment

The number of intraspecific Arctic Loon encounters was higher during the period with destroyed nests than during the pre-laying period which was also higher than the encounter-rate during incubation and brood-rearing periods (section II.1.D). Encounters were longer on territories with destroyed nests than during the pre-laying period.

A similar pattern occurred for Red-throated Loons although the number of encounters was the same on failed nests as during the pre-laying period. However, the average duration of the encounters was longer on failed territories than during the pre-laying period and they often contained sustained aerial components (section II.2.D).

Thus both species spent more time in intraspecific encounters after the nest was lost than when territories were re-occupied in the spring. It is reasonable to assume that territorial strife would be highest during the period of territorial selection.

The three behaviour patterns discussed all required a significant amount of time and energy. It seems likely that these behaviours (territory occupation after nest loss; roving summer flocks visiting these territories; and increased territorial encounters after nest loss) must have some function in order to justify the energy expenditure. The most logical function was the establishment of territories during the summer when time was available to failed and non-breeders. The behaviour presumably gave the individual an advantage in the spring when time for territorial establishment was short and selection worked against prolonged territorial strife.

An indication that territories were in fact selected prior to the breeding season was provided by the pattern of pond occupation in the spring. Ponds near the coast attained normal water levels after those further inland, due to annual flooding of the McConnell River. However, loons did not all try to nest on the inland ponds which would be selectively favoured due to a longer available breeding season. A stronger selective pressure favoured nesting nearer the coastal food source (section III) and this required a slightly delayed beginning of nesting. Birds nesting near the coast must have been familiar with the area in order to know that suitable nest ponds were available under the flood waters and were worth waiting for.

APPENDIX 2

ESCAPE REACTIONS OF ADULT LOONS

This analysis tests for specific differences in escape behaviour and the modifying effect of environment (pond-size).

In the course of routine nest visits the behaviour of the attendant adult loons was noted. It was assumed that reactions to man were representative of behaviour when Timber Wolves or Arctic Foxes approached the nest ponds. This assumption was reasonable based on the reactions of loons to foxes, as observed from observation towers.

The analysis is based on 504 visits to 88 Red-throated Loon nests and 364 visits to 91 Arctic Loon nests in three years on the main McConnell River study area. There was an average of 5.7 visits per Red-throated Loon nest and 4 visits per Arctic Loon nest. A visit was counted only when the observer actually reached the nest or shore of the pond. Nests observed from a distance were not counted. When the purpose of the visit was to catch young loons, the visit was not counted if the adults reacted differently after the observer entered the water.

Four pond size-ranges were recognized: less than 0.5 ha; 0.5 ha to but not including 1.0 ha; 1.0 ha to but not including 2.0 ha; and over 2.0 ha.

It seemed probable that the escape behaviour of the adults would change during the different stages of the reproductive cycle. Hence, it was necessary to test the number of visits to each pond size during each reproductive stage in order to insure that the ratio of visits per pond size was the same for each stage.

The data appear in tables 73 and 74 which omit visits to nests in which loons were incubating infertile eggs past the normal hatching time. The ratio of visits to each pond size was the same for each reproductive period of the Arctic Loon ($\chi^2 = 10.30$; df = 9; $P>0.1$). Data for pre-egg stage were too few and this row was omitted.

There were no Red-throated Loons on ponds over 2.0 ha and this column was omitted from table 74. Inclusion of rows for pre-egg and destroyed nests resulted in too many low expected values and these rows were not included. The remaining data (84% of the total) showed no differences in the rate of visitation to different pond sizes for each reproductive period ($\chi^2 = 2.44$; df = 4; P is NS). Thus, it was possible to analyze escape reactions directly with regard to pond-size.

The reactions of adult loons were grouped into three classes: 1) the adult(s) stayed on the pond during the visit; 2) one adult stayed and the other flew; 3) all adults flew from the pond. The three categories probably reflect the motivational state of the birds in terms of their

TABLE 73

NUMBER OF VISITS TO ARCTIC LOON NEST PONDS OF VARIOUS SIZES DURING EACH REPRODUCTIVE STAGE

Stage of reproductive cycle	Size of pond (ha)				Totals
	less than 0.5	0.5-1.0	1.0-2.0	over 2.0	
Pre-egg	0	2	1	2	5
Incubation	9	18	41	60	128
Hatching	0	6	11	14	31
Young	7	18	24	50	99
Eggs or young destroyed	10	9	23	54	96
Totals (excluding pre-egg stage)	26	51	99	178	354

TABLE 74

NUMBER OF VISITS TO RED-THROATED LOON NEST PONDS OF VARIOUS SIZES DURING EACH REPRODUCTIVE STAGE

Stage of reproductive cycle	Size of pond (ha)				Totals
	less than 0.5	0.5-1.0	1.0-2.0	over 2.0	
Pre-egg	21	1	3	0	25
Incubation	174	21	13	0	208
Hatching	45	2	2	0	49
Young	131	16	8	0	155
Eggs or young destroyed	47	3	2	0	52
Totals	418	43	28	0	489

tendency to flee when threatened.

It was not always possible to record the reactions of adults especially when working in areas of high nest pond concentrations. In these areas the observer occasionally caused escape behaviour by adults on one pond while he was actually visiting a different pond and was unable to record the reactions. This accounts for the differences in the totals in the various tables.

Escape Behaviour of Arctic Loons

The responses of adult Arctic Loons to visits to their nest ponds are tabulated in table 75. The ratio of the three classes was tested for all pond sizes in a 4 X 3 contingency table. There was a significant difference in the ratios over the four pond sizes ($\chi^2 = 34.49$; df = 6; $P<0.005$). The data were then partitioned to isolate those differences.

Sixty-eight per cent of the above chi-square was caused by the class of ponds under 0.5 ha. This column was eliminated and the three larger pond sizes were tested. A significant interaction was found ($\chi^2 = 9.79$; df = 4; $P<0.05$) and was due to ponds between 0.5 and 1.0 ha (73% of χ^2). This column was then eliminated and the two classes with the largest sized ponds were tested and no difference in escape reactions was found ($\chi^2 = 1.06$; df = 1; P is NS).

The two classes with the smallest pond sizes were then tested for differences. Unfortunately the expected

TABLE 75

NUMBER OF OCCURRENCES OF EACH TYPE OF BEHAVIOUR FOR EACH POND SIZE, BY ARCTIC LOONS

Escape behaviour of adults	Pond size (ha)				Totals
	less than 0.5	0.5-1.0	1.0-2.0	over 2.0	
Adult(s) stay	1	21	55	83	160
One stays and one flies	2	4	3	9	18
Adult(s) fly	15	21	19	32	87
Totals	18	46	77	124	265

values were low for the class where one adult flushed and the other stayed on the pond. This was overcome by dividing this class equally between the other two classes and forming a 2 X 2 contingency table. The adult behaviour was significantly different for each pond size ($\chi^2 = 8.22$; df = 1; $P<0.005$).

Arctic Loons were more likely to fly when pressed on the smallest ponds (less than 0.5 ha) than on ponds between 0.5 and 1.0 ha. They were also more prone to flush from ponds of this latter size than from ponds over 1.0 ha. There was no difference in the reactions on ponds between 1.0 and 2.0 ha and those over 2.0 ha. Thus, the escape behaviour of Arctic Loons was directly modified by the size of the nest pond.

Escape Behaviour of Red-throated Loons

The escape reactions of adult Red-throated Loons are presented in table 76. There were no nest ponds over 2.0 ha and this column was eliminated.

It was evident that the escape behaviour varied with the size of the nest pond ($\chi^2 = 160.13$; df = 4; $P<0.005$). Fully 92% of the chi-square was caused by class of ponds larger than 1.0 ha. When this class was ignored and the remaining two were tested, it was found that there was no difference between the two classes under 1.0 ha ($\chi^2 = 0.073$; df = 2; P is NS). Thus Red-throated Loons were more apt to

TABLE 76

NUMBER OF OCCURRENCES OF EACH TYPE OF BEHAVIOUR FOR EACH POND SIZE, BY RED-THROATED LOONS

Escape behaviour of adults	Pond size (ha)				Totals
	less than 0.5	0.5-1.0	1.0-2.0	over 2.0	
Adult(s) stay	26	3	28	0	57
One stays and one flies	11	1	1	0	13
Adult(s)	305	37	3	0	345
Totals	342	41	32	0	415

stay on nest ponds over 1.0 ha and were more likely to flush from ponds smaller than 1.0 ha.

Comparison of Escape Behavior of Arctic and Red-throated Loons

The overall data for each species indicated substantial differences in the escape behaviour of the two species (χ^2 = 179.42; df = 2; P<0.005 for the H_o; 160:18:87 = 57:13:345). These differences were not strictly species-specific but were modified by pond size. This section compares the species for each pond size and isolates those differences which were unaffected by the environment.

The two species showed no difference in tendency to flush from ponds below 0.5 ha (χ^2 = 0.088; df = 1; P is NS for the H_o; 2:16 = 31:312). The small expected values caused by the category where one adult flushed and the other stayed, necessitated equal division of this category between the other two groups. The clear-cut results suggest that the method was valid for this data.

Analysis of ponds between 0.5 and 1.0 ha revealed that Red-throated Loons were significantly more likely to fly when approached whereas Arctic Loons tended to stay on the pond (χ^2 = 18.45; df = 1; P<0.005 for the H_o; 23:23 = 4:37). The data for the 'one adult flush - one adult stay' category were again divided due to small sample size and yielded clear-cut results.

Comparison of all ponds over 1.0 ha revealed no

differences in tendency of either species to fly when approached ($\chi^2 = 4.82$; df = 2; P is NS).

The large specific differences in escape behaviour disappeared when the data were corrected for environmental factors. Both species were equally likely to flush from very small ponds and equally likely to stay on the larger ponds. The only specific differences occurred on ponds between 0.5 and 1.0 ha where Red-throated Loons tended to fly and Arctic Loons tended to stay when disturbed.

APPENDIX 3

COMPARISON OF TERRITORIAL BEHAVIOUR OF ARCTIC AND RED-THROATED LOONS

Arctic and Red-throated Loons spent relatively little time in territorial defense (sections II.1.D and II.2.C). These apparently efficient systems are compared in this section.

The number of territorial encounters was examined for each species for each stage of the breeding cycle. The number of hours with and without encounters were compared for the data from tables 24 and 31. There was no difference in the number of intraspecific encounters for each species for the pre-laying stage ($\chi^2 = 0.796$; df = 1; P is NS for the H_o; 54:786 = 20:370); incubation stage ($\chi^2 = 1.77$; df = 1; P is NS for the H_o; 13:850 = 3:451); brood rearing stage ($\chi^2 = 0.297$; df = 1; P is NS for the H_o; 8:274 = 12:310); and the stage where eggs or young were lost ($\chi^2 = 2.85$; df = 1; $P<0.10$).

There were no differences in the number of encounters but there were differences in their duration (tables 25 and 32). Territorial encounters among Arctic Loons were significantly longer than those of Red-throated Loons for the pre-laying stage ($t = 3.29$; df = 45; $P<0.01$) and brood-rearing stage ($t = 2.44$; df = 15; $P<0.05$). The data for the incuba-

tion stage showed a similar trend but was not significant ($t = 1.12$; $df = 11$) due to the small sample size for Red-throated Loons.

The overall comparison of the amount of time spent in intraspecific territorial defense is presented in table 77 where the data are grouped by minutes with and without territorial encounters. Arctic Loons spent a much higher proportion of their time defending territories than did Red-throated Loons. This held for the pre-laying period ($\chi^2 = 117.36$; $df = 1$; $P<0.005$) and incubation period ($\chi^2 = 32.99$; $df = 1$; $P<0.005$) but not for the brood-rearing period ($\chi^2 = 3.02$; $df = 1$; $P<0.10$). These differences were primarily due to the duration of encounters.

Another aspect of the territorial behaviour of the two species involved calling at conspecifics which flew over or near the territory. Red-throated Loons 'roll-growled' and 'wailed' (Huxley 1923; Drury 1961) at flying conspecifics causing the potential intruders to change course and fly away. Arctic Loons used their plaintive call described by Sutton (1932:14) as 'ah-hah-wee' or a clear 'oo-loo-lee' (Sutton and Parmalee 1956).

A sample of reactions to flying conspecifics by territory holders was taken during the pre-laying period in 1969. The data are presented in table 78 and are grouped according to whether residents called at flying loons. Red-throated Loons were more likely to call at flying conspecifics

TABLE 77

PROPORTION OF TIME SPENT IN TERRITORIAL DEFENSE BY ARCTIC AND RED-THROATED LOONS

	Arctic Loons			Red-throated Loons		
	Number of minutes		Proportion of time in encounters	Number of minutes		Proportion of time in encounters
	with encounters	with no encounters		with encounters	with no encounters	
Pre-Laying	540	49890	0.0107	69	23301	0.0029
Incubation	92	51688	0.0018	7	27263	0.0003
Brood-rearing	30	16890	0.0018	21	19299	0.0011
Totals	662	118468	0.0056	97	69863	0.0014

TABLE 78

REACTIONS OF TERRITORIAL LOONS
TO FLYING CONSPECIFICS

	Reaction of resident Loons		Totals
	call	no call	
Arctic Loon	19	13	32
Red-throated Loon	25	3	28
Totals	44	16	60

than were Arctic Loons ($\chi^2 = 6.83$; df = 1; $P<0.01$). Red-throated Loons placed greater stress on vocal threats and this may have been related to their small nest ponds. Displays could be more dangerous in the cramped conditions of the small ponds than on larger ponds. The faster eviction of intruders may also be a function of the small pond size used by Red-throated Loons.

The importance of considering the ecology of a species when analyzing its behaviour has also been stressed by several other workers (Cullen 1957; Haartman 1957; Tinbergen 1959, 1967; Crook 1964, 1965, 1970; Lack 1967, 1968; Simmons 1967, 1970).